UPPER SILURIAN AND LOWER DEVONIAN SPORE ASSEMBLAGES FROM THE WELSH BORDERLAND AND SOUTH WALES

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ABSTRACT. A reconnaissance of some Wenlockian, Ludlovian, Downtonian, and Dittonian strata from type and other sections in England and Wales revealed a variety of spore assemblages dominated by small, trilete, azonate, retusoid, sculpturally varied spores. The spore sequence is described. In the Welsh Borderland sections two striking changes occur in spore assemblage composition; (*a*) at the Ludlovian–Downtonian boundary, and (*b*) between the Downtonian and Dittonian; available evidence suggests that these vertical changes are essentially time-controlled whereas environmental effects are mainly reflected in the relative abundance of spores to acritarchs and other marine microfossils. Assemblages from South Wales are generally poorly preserved and therefore only limited comparisons are possible with the Welsh Borderland sequences. Published data on comparable horizons from other areas is limited but shows essentially the same sequence of spores in late Silurian and early Devonian strata as that shown here, thus emphasising the stratigraphic significance of these results. The potential usefulness of spores and microplankton for linking vertebrate-zoned continental strata with invertebrate-zoned marine sequences is emphasized.

Forty-nine different types of spore are described, two genera *Streelispora* and *Synorisporites*, twenty species, and four varieties are regarded as new.

A PRELIMINARY study of Upper Silurian and early Devonian strata from England and Wales has revealed the presence in many of these rocks of abundant well-preserved spores and microplankton. The main sections studied in the area are the type Ludlovian section at Ludlow (Shropshire), the comparable section near Millichope (Shropshire), and Downtonian from the Ludford Lane and Downton Gorge sections. In addition to the Ludlow area, Upper Silurian and Lower Devonian strata have been studied at Gorsley Common and Perton Lane (Herefordshire), Usk (Monmouthshire), Cwm Dwr and Sawdde Valley (Carmarthenshire), and Freshwater East (Pembrokeshire). Material has been obtained also from probable Temeside shales, Long Mountain (Shropshire), and Dittonian strata, Brown Clee Hill (Shropshire). All the localities investigated are listed in the appendix at the end of the paper.

One of the authors (T. R. L.) is engaged in a study of the microplankton and has been responsible for extraction and study of the Silurian material from Ludlow, Millichope and Usk. Richardson has studied Lower Devonian strata from Ludlow, Long Mountain, Brown Clee Hill and Upper Silurian and Lower Devonian strata from Gorsley, Downton Gorge and Freshwater East. Both authors have collected and studied material from the Cwm Dwr and Sawdde Valley sections.

In general, preservation of spores is good and occasionally excellent in the Welsh Borderland samples especially in the Downtonian and Dittonian, and is poor in south-west Wales. Spores have not been found in many of the samples processed from the Sawdde, Cwm Dwr, and Freshwater East sections and identification of spores when present is difficult because they are carbonized and poorly preserved. Consequently only general comparisons are possible at this stage with the type Ludlovian–Downtonian assemblages. Nevertheless there are some indications that even in this area spores may eventually provide significant stratigraphic contributions.

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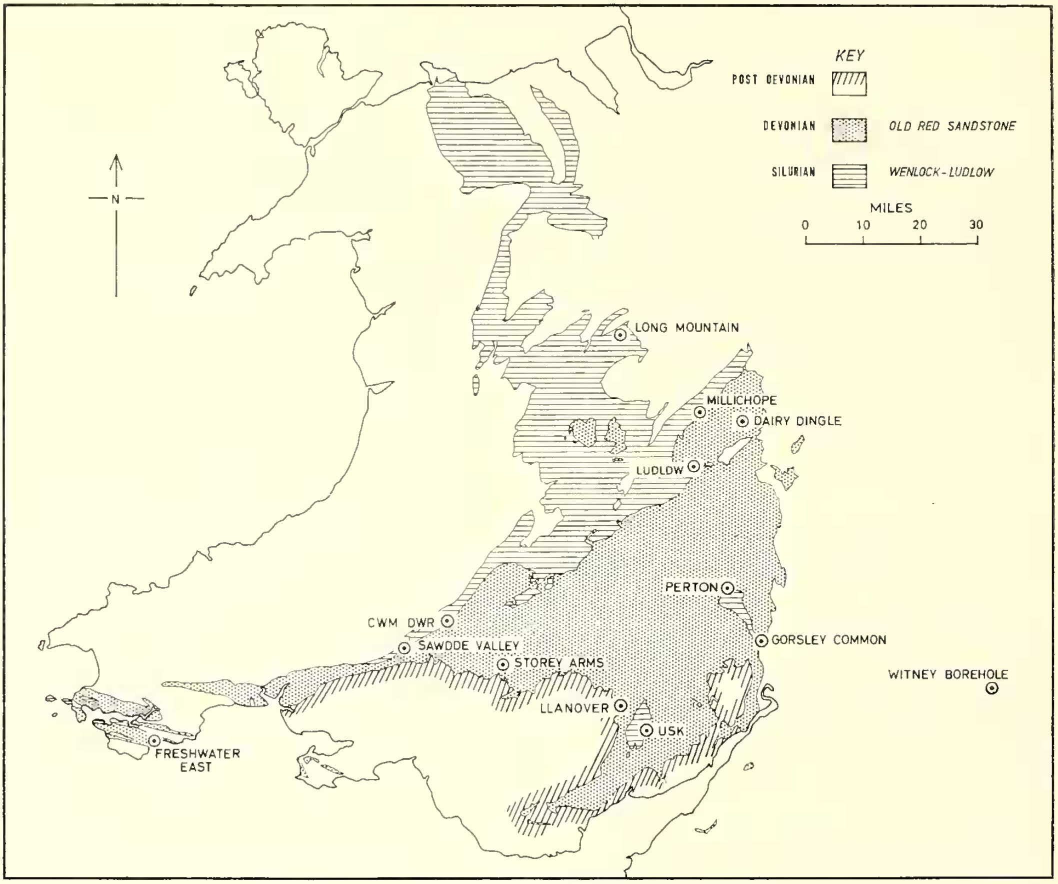


TEXT-FIG. 1. Location of the main sampling areas.

SILURIAN MIOSPORES FROM THE WELSH BORDERS

Miospores are present in small numbers throughout the Ludlow succession of the type area and are always associated with abundant acritarchs, chitinozoa, and scolecodonts; they form less than 1% of most assemblages rarely figuring in counts of 200–300 individuals. Of the fifty-six samples examined from the Ludlow succession thirty-seven yielded spores.

The Ludlovian spore succession from the type area is shown in Table 1. Supplementary information has been obtained from a sequence collected from the Millichope–Diddlebury area (stratigraphic control supplied by Dr. J. H. Shergold) and the spore sequence from this area is presented in Table 2. Spores were also recovered from the Wenlock Shale and Upper Llanbadoc Beds of Usk and from the Eltonian (probably Middle Eltonian) of Ledbury (see Table 3).

TABLE 1. Distribution of spores through the Ludlovian and Lower Downtonian of the type area, Ludlow, Shropshire. W.L., Wenlock Limestone; L.E.B., M.E.B., and U.E.B., Lower, Middle, and Upper Elton Beds; L.B.B., and U.B.B., Lower, and Upper Bringewood Beds; L.L.B. and U.L.B., Lower and Upper Leintwardine Beds; L.W.B. and U.W.B., Lower and Upper Whitcliffe Beds; D.C.S., Downton Castle Sandstone Group. Silurian samples have the prefix LD (Appdx. A)

	SILURIAN																																																							DEVONIAN					
Horizon	W.L.			L.E.B						M.E.B					U.E.B						L.B.B						U.B.B					L.L.B								U.L.B				L.W.B						U.W.B						D.C.S					
Spore Species / Sample No.	57	59	1	2	3	54	54A	54B	53	50	43	44	45	45B	46	49	5	47A	47B	48	56	58	6	7	8	9	10	11	12	55	41	13	13B	14	15	16	16B	17	34	35	18	36	19	20	33	32	31	30	29	28	26A	25	23	22	40	LU1	DC2A	DC3A	LU2	LU3	DC5A
R. cf. warringtonii		?		X	X		X		X	X				X	X					X	X						X												X	X	X		X			X							X				X	X		?	X
Ambitisporites cf. dilutus		X		X	X		X	X	X	X	X					X			X																																										
A. chulus var chulus																																																		X		X	X	X		X	X	X	X	X	X
A. chulus var. inframurinatus				X			X					X		X	X	X	X	X	X	X				X	X	X				X					X					X						X		X	X	X	X		X	X		X	X	X	X		
cf. Synarisparites verrucatus							X		X											X																																									
A. chulus var. nanus		X		X	X				X		X	?		X				X	X																																							X	X	X	X
cf. Synorisporites downtanensis									X					X												X																																			
cf. Streelispora granulata														X																																												X	X	X	X
Retusatriletes sp. A																X																																				X				X		X	X		X
Apiculiretusispara synorea																										X																														X	X	X	X	X	X
Apiculiretusispora sp. C																																								X				X													X	?		X	X
Apiculiretusispora spicula																																																								X	X	X	X	X	X
Retusotriletes cf. minar																																																								X	?	X	X	X	X
Synorisporites downtanensis																																																								X	X	X	X	X	X
S. tripapillatus																																																								X		X	X	?	X
S. verrucatus																																																								X		X	X		X
? Archaeozonatriletes cf. divellamedium																																																								X		X	X	X	X
Cymbosporites echinatus																																																								X	X	X	X	X	X
C. verrucosus																																																								X	X		X	X	X
? Perotrilites sp. A																																																								X			X		X
Retusotriletes dubius																																																									?	?			
Apiculiretusispora sp A																																																									X	X			X
Emphanisparites cf. micrarnatus																																																									X	X		X	?
? Archaeozonatriletes dubius																																																									X				X
Retusotriletes warringtanii																																																										X			X
Emphanisparites micrornatus																																																										?			?
E. cf. neglectus																																																											X		X

Nature of the record. The Ludlovian spore record is fragmentary and undoubtedly a somewhat imperfect record of the true Ludlovian spore flora. Despite intensive search several of the 15 components recorded are represented either by single specimens, or by only two or three specimens. The scant record is undoubtedly a function primarily of the long distance of the Ludlow region from the Ludlovian shore lines, and it is reasonable to suppose that a near-shore or limnic sequence would yield a far more abundant spore flora of appreciably greater diversity. This is to a certain extent indicated by the

TABLE 2. Distribution of spores through the Wenlockian and Ludlovian of the Millichope–Diddlebury area Shropshire. W.S., Wenlock Shale; U.C.B., Upper Coalbrookdale Beds; T.B., Tickwood Beds; other abbreviations as for Table 1. All samples have the prefix MD (Appdx. A)

Spore Species	WS ucb	WS tb	WL	LEB			MEB	UEB		LBB	UBB		LLB		LWB			UWB	
Sample N^o^.	41	40	38	8	9	12	14	5B	6	16B	19	17	3B	24	26	30	31	33	34
? Archaeozonotriletes cf. divellomedium	X				?													?	
Ambitisporites dilutus s.s.	X	X	X																
Ambitisporites cf. dilutus	X	X	X	X	X	X			?										
Am. cf. avitus		X																	
A. chulus var. chulus								X	X			X						X	X
A. chulus var. inframurinatus			?					X	X		X	X							X
cf. Synorisporites verrucatus			X																
Retusotriletes cf. warringtonii				X	X		X	X	X		X	?		?					
cf. Synorisporites downtonenisis					X			X											
? Apiculiretusispora sp. D																			X

evidence from Usk which, according to the present palaeogeographic reconstruction (Holland and Lawson 1963) lay fairly close to the Ludlovian shore-line. Large numbers of spores were recovered from both the Wenlock Shale sample and the sample from the Upper Llanbadoc beds (Lower Leintwardine) (spores totalled approximately 90% and 20% respectively of the total assemblage). Neither of these assemblages, however, despite their richness of numbers, exhibited any greater diversity of spore types, which suggests that the total recorded spore flora is more representative than might at first be thought. The Millichope–Diddlebury sequence (Table 2) little more than confirmed the main Ludlow succession, adding only ? *Archaeozonotriletes* cf. *divellomedium* Chibrickova 1959 and the spiny tetrad ? *Apiculiretusispora* sp. D (single specimen).

This evidence suggests that although continuity of the record would certainly be improved by examination of further successions the number of spore types would not be greatly increased. It seems important to establish this point before any fair comparison of the Ludlovian with the Downtonian spore flora is attempted.

Stratigraphic interpretation. This can only be tentative in view of the discontinuous nature of the record. Nevertheless some of the vertical changes appear to be evolutionary, rather than an artefact of the imperfect record or a product of facies control. Thus in the Wenlock Shale all the spores seen were smooth, simple triradiate types. The Wenlock

Limestone heralds the appearance of the atypical *Ambitisporites dilutus* (Hoffmeister) comb. nov. i.e. *A.* cf. *dilutus* with raised laesurae, and the sculptured form cf. *Synorisporites verrucatus* sp. nov. makes its entry. *A. chulus* var. *nanus* var. nov. and *A. chulus* var. *inframurinatus* var. nov. also appear for the first time but are thinner walled than the specimens from higher horizons. These give way to somewhat more typical forms in the Lower Elton Beds though they still tend to be small in size with narrow borders and relatively thin distal hemispheres. In the Upper Elton Beds and higher in the succession the latter have wider zones of equatorial thickening and thick-walled distal hemispheres, and more sculptured forms appear.

TABLE 3. Spores present in two samples from the Usk Inlier, and one from Ledbury. W.S., Wenlock Shale; U.L.B., Upper Llanbadoc Beds; E.B., Elton Beds

	Ledbury	*Usk*	
	E.B.	*W.S.*	*U.L.B.*
Retusotriletes cf. *minor*	×	—	—
Archaeozonotriletes chulus var. *inframurinatus*	×	—	×
A. chulus var. *nanus*	×	×	×
A. chulus var. *chulus*	—	—	×
Ambitisporites dilutus s.s.	—	×	—
A. cf. *dilutus*	—	—	×
Retusotriletes cf. *warringtonii*	—	×	×

DEVONIAN MIOSPORES FROM THE WELSH BORDERLAND

In contrast to the underlying Silurian, spores are frequently abundant in Devonian strata from South Wales and the Welsh Borderland. Preservation is generally good in the Welsh Borderland (Shropshire and Herefordshire) but relatively poor in samples examined from Carmarthenshire and Pembrokeshire. For the purposes of this paper the base of the Devonian in the Welsh Borderland is taken at the Ludlow Bone Bed at Ludford Lane, Ludlow, and its equivalents elsewhere. Consequently the Downtonian is included within the Devonian.

Downtonian

Samples (see Table 4) from the Downton Castle Sandstone Group, Ludford and Downton Gorge (Shropshire), Gorsley Common and Perton Lane (Herefordshire), and ?Temeside Shales, Wallop Hall quarry, Long Mountain (Shropshire), have all yielded abundant well-preserved spores. In contrast Downtonian equivalents in the Cwm Dwr section (Capel Horeb quarry) have so far yielded only poorly preserved spores. The only other samples yielding spores of approximately this age in South Wales are those of the Lower Red Marl Group on the north side of Freshwater East but these contain assemblages in which most of the spores are carbonized.

Localities in the Welsh Borderland at Ludlow, Gorsley, Perton Lane, and Long Mountain have yielded essentially the same spore assemblages; those at Gorsley and Ludlow are practically identical. At the Perton Lane and Long Mountain localities several of the rarer species have not been found but most of the species which are common at the other two localities occur (Table 4). All the assemblages from the Lower Downtonian form a pronounced contrast with those from the Wenlockian and Ludlovian (Tables 1 and 5).

TABLE 4. Comparison between Basal Downtonian assemblages from Gorsley, Ludlow, Perton Lane, and ? Temeside Shales, Long Mountain (Shropshire)

	Ludlow				
	Ludford Lane	*Downton Gorge*	*Gorsley*	*Perton Lane**	*Long Mountain**
Retusotriletes dubius	?	?	×	—	—
R. cf. *warringtonii*	×	×	×	×	×
R. warringtonii	×	×	×	×	—
R. cf. *minor*	×	×	×	×	×
R. sp. A	×	×	×	—	—
Apiculiretusispora spicula	×	×	×	—	—
A. synorea	×	×	×	×	×
A. sp. A	×	×	×	—	—
A. sp. C	×	—	×	—	—
? *Dictyotriletes* sp. B (*Dictyotidium*)	×	—	×	—	—
cf. *Streelispora granulata*	×	×	×	—	—
Synorisporites downtonensis	×	×	×	—	—
S. tripapillatus	×	×	×	×	×
S. verrucatus	×	×	×	×	×
Emphanisporites micrornatus	?	—	?	—	—
E. cf. *micrornatus*	×	—	×	—	×
E. cf. *neglectus*	×	×	×	×	—
A. chulus var. *chulus*	×	×	×	×	×
A. chulus var. *inframurinatus*	×	×	×	—	—
A. chulus var. *nanus*	×	×	×	?	×
? *A.* cf. *divellomedium*	×	×	×	?	—
? *A. dubius*	×	—	×	?	—
Cymbosporites echinatus	×	×	×	×	×
C. verrucosus	×	×	×	×	×
? *Perotrilites* sp. A	×	—	×	—	×
Other acid resistant microfossils					
Acritarchs	×(D)	×(D)	×(D)	×	—
Chitinozoa	×	×	—	—	—
Hoegispheres	×	×	—	—	—
Scolecodonts	×	×	—	—	—

(D) = decreasing rapidly upwards in proportion to spore content.
* = based on a single sample.

Changes at the Ludlow Bone Bed

At the Ludlovian–Downtonian boundary there is a sharp facies change from deposits representing open-sea conditions to those of near-shore–beach (Allen and Tarlo 1963). Paralleling this change there is a significant change in the relative abundance of spores to acritarchs. In the Silurian, spores generally constitute less than 1% of most assemblages and they are associated with abundant acritarchs, chitinozoa, and scolecodonts. In the basal Downtonian at Ludlow and Gorsley, however, acritarchs decrease rapidly upward in the succession in relation to the spores. At Ludlow for instance the following have been recorded from above the Ludlow Bone Bed (P = Present):

	Spores	*Acri-tarchs*	*Chitinozoa*	*Scolecodonts*	*Hoegi-spheres*	*Indeter-minate*
LU 3 (5 ft. 10 in.–6 ft. above LBB)	70%	12%	—	—	—	18%
LU 2 (4 ft. 10 in.–5 ft. above LBB)	51%	36%	—	—	P	13%
LU 1 (0–4 in. above LBB)	11%	81%	P	P	P	8%

Since acritarchs and chitinozoa are often abundant in holomarine, and absent from fluviatile and fresh water, environments, these changes suggest a transition from marine to brackish water. The same conclusion was reached by Allen and Tarlo (1963, p. 135) based on sedimentological studies. No acritarchs have so far been seen in the Temeside shales, but only one sample from this group has yielded microfossils.

As well as the increase in the relative abundance of the spores there is also an increase in variety. Twenty-four different types of spore have been recorded from the Downtonian

TABLE 5. Comparison between Upper Whitcliffe and Basal Downtonian assemblages, Linton Quarry, Gorsley Common

Species	*Silurian* *Upper Whitcliffe Beds*	*Devonian* *Lower Downton Castle Sst. Gp.*
Retusotriletes cf. *warringtonii*	×	×
Dictyotriletes sp. B (*Dictyotidium*)	×	×
A. chulus var. *inframurinatus*	×	×
Retusotriletes dubius	—	×
R. cf. *minor*	—	×
R. sp. A	—	×
Apiculiretusispora spicula	—	×
A. synorea	—	×
A. sp. A	—	×
A. sp. C	—	×
cf. *Streelispora granulata*	—	×
Synorisporites downtonensis	—	×
S. tripapillatus	—	×
S. verrucatus	—	×
Emphanisporites micrornatus	—	×
E. cf. *micrornatus*	—	×
E. cf. *neglectus*	—	×
A. chulus var. *chulus*	—	×
A. chulus var. *nanus*	—	×
? *A.* cf. *divellomedium*	—	×
? *A. dubius*	—	×
Cymbosporites echinatus	—	×
C. verrucosus	—	×
? *Perotrilites* sp. A	—	×
Acritarchs	× (A)	× (D)
Chitinozoa	×	—
Hoegispheres	×	—
Scolecodonts	×	—

(A), greater than 80% of the spore–acritarch content.
(D), decreasing rapidly upward in relation to the spore content.

belonging to eight spore genera. In contrast fifteen different spore species and forms are recorded in the Wenlock and Ludlovian belonging to six spore genera.

Genera recorded in the Wenlockian and Ludlovian are *Retusotriletes*, *Ambitisporites*, *Archaeozonotriletes*, *Apiculiretusispora*; and possible representatives of two new genera (cf. *Synorisporites verrucatus* and cf. *Streelispora*). There is also a form which is doubtfully referred to the genus *Dictyotriletes* (? *Dictyotriletes* sp. B).

In the Downtonian on the other hand *Ambitisporites* has not been found and in addition to those mentioned above further genera present are *Emphanisporites* (rare forms with fine proximal ribs), *Cymbosporites* (patinate forms with spinose and verrucate sculpture), and ?*Perotrilites* (spores with two clearly separated membranes). *Perotrilites* has a structural organization so far not seen in the Silurian and one which is rare in the Downtonian.

Perhaps the greatest contrast between the Wenlockian–Ludlovian and Downtonian assemblages is the increase in the number of sculptured forms. No sculptured forms have so far been found in the Wenlock Shales. In the Wenlock Limestone so far only a single specimen has been found with verrucate sculpture. In the succeeding Ludlovian, verrucate, murinate, granulate, and apiculate sculpturing has been found but specimens with any sculpture at all are rare and the majority of forms found in any one sample are smooth walled. The Downtonian on the other hand contains abundant sculptured spores, and verrucate, murinate, granulate, and apiculate types of sculpturing are all relatively common.

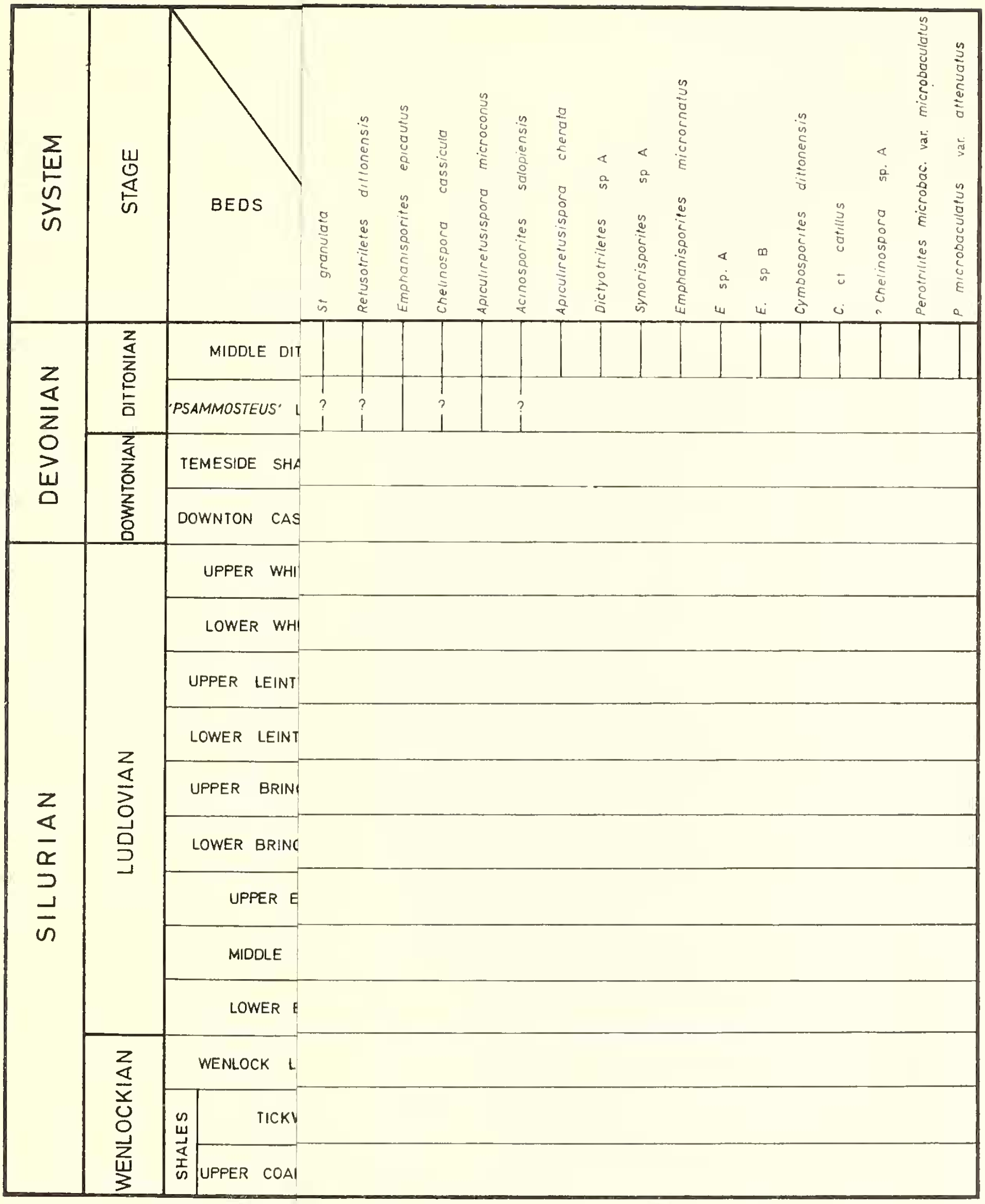
Dittonian assemblages

A sample from the '*Psammosteus*' Limestone Group (Downtonian/Dittonian junction near Newport, South Wales) was described by Chaloner and Streel (1968) and has been re-examined. Although the preservation is relatively poor, this assemblage shows several of the species important in the succeeding Ditton Group but lacks the most characteristic species of the Downtonian.

A feature of importance is that the genus *Emphanisporites* becomes much more common. In the Downtonian the presence of proximal ribs is a rare and poorly developed feature. In the '*Psammosteus*' Limestone Group, many more spores of this type occur. However, the presence of proximal ribs still appears to be an 'unstable' character since in spores which are otherwise identical there are some that have fine proximal ribs and others that do not.

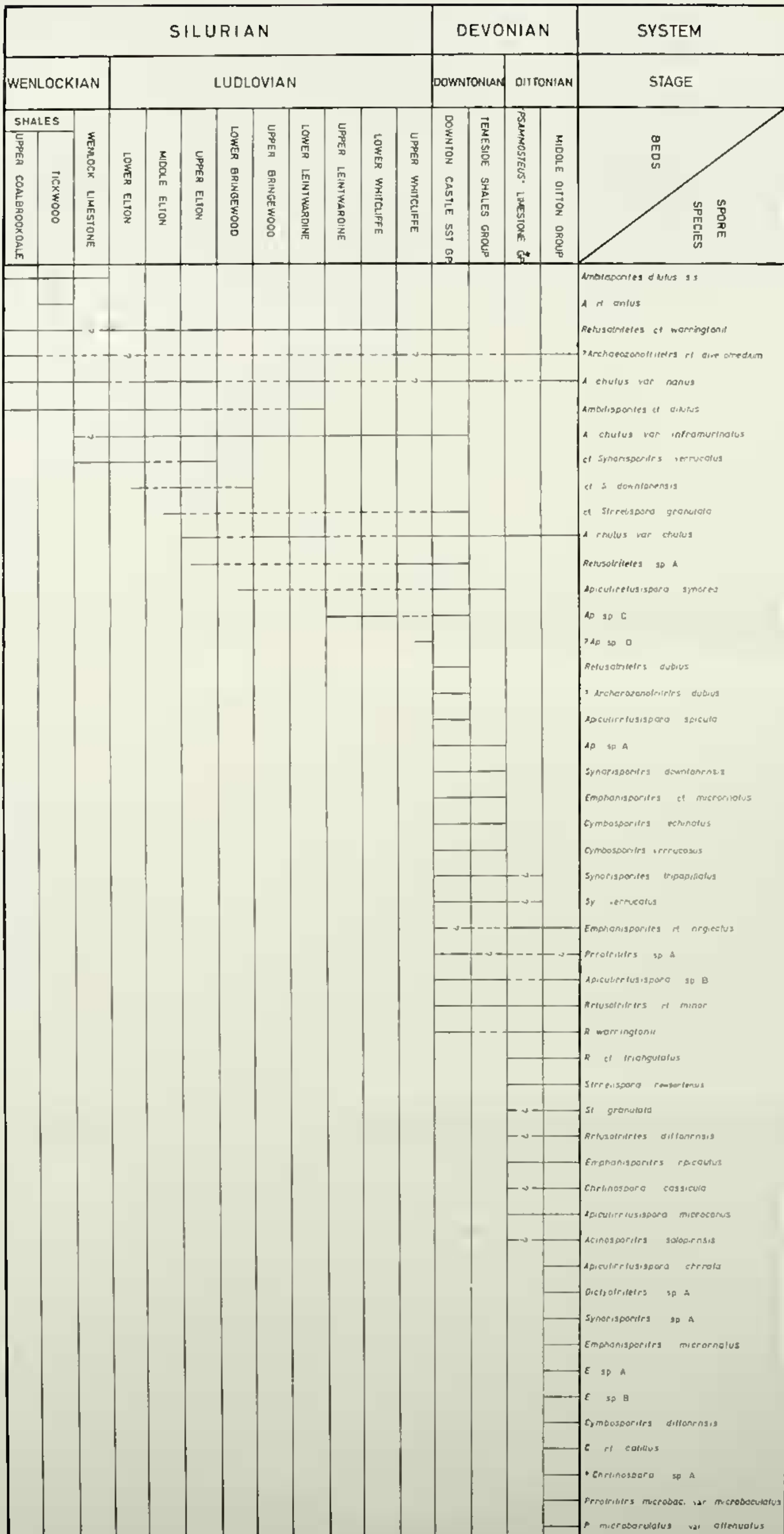
Two distally smooth-walled types of *Emphanisporites* (*E.* cf. *neglectus* Vigran 1964 and *E. epicautus* sp. nov.) occur in the '*Psammosteus*' Limestone; they are referred to *E. rotatus* McGregor 1961 by Chaloner and Streel (1968), who record that of their five common species *E. rotatus* constitutes 23% of the spore assemblage. However, this may be a somewhat high figure since the preservation is relatively poor and *Emphanisporites* is an easily recognizable spore type.

From the Ditton Group an assemblage approximately 800 ft. above the '*Psammosteus*' Limestone, has yielded abundant well-preserved spores which have helped in interpreting the poorer assemblage from the '*Psammosteus*' Limestone Group. Six species and varieties are found here which are not recorded in the '*Psammosteus*' Limestone Group. In addition five other forms represented by relatively few specimens are identified only



TEXT-FIG. 2. Rang escribed by Chaloner and Streel (1968) and re-examined.

TEXT-FIG. 2. Range chart showing spore distribution in the Silurian and Early Devonian of the Welsh Borderland and South Wales.* Based on a sample described by Chaloner and Streel (1968) and re-examined.



TEXT-FIG. 2. Range chart showing spore distribution in the Silurian and Early Devonian of the Welsh Borderland and South Wales.* Based on a sample described by Chaloner and Streel (1968) and re-examined.

to generic level; they represent new species but too few specimens have been found. *Emphanisporites* is abundant and a variety of forms with distal sculpture occur.

COMPARISONS BETWEEN DOWNTONIAN AND DITTONIAN ASSEMBLAGES

The range chart (text-fig. 2) shows distinct differences between the Downtonian and Dittonian assemblages. Species of the genera *Cymbosporites*, *Synorisporites*, *Perotrilites*, and particularly *Emphanisporites* show the greatest contrasts. Only rare specimens of *Emphanisporites* with smooth or apiculate distal surfaces occur in the Downtonian, whereas in the Dittonian specimens of this genus are relatively common and show greater variety. The genera *Acinosporites* and *Chelinospora*, and several other distinctive species, e.g. *Retusotriletes* cf. *triangulatus* Streel 1967, and *Streelispora newportensis* (Chaloner and Streel) comb. nov., have not been found in the Downtonian and are most common in the Ditton Group.

GENERAL CONSIDERATIONS

In the Welsh Borderland succession Silurian of open marine facies is followed by Downtonian marginal-marine to fluviatile facies, and Dittonian fluviatile facies. Such facies differences will obviously affect the nature and composition of spore assemblages. Since most trilete spores were probably produced by land vascular plants nearness to the shore, mouths of rivers, etc., will be reflected by spore abundance and possibly variety. However, there is some evidence that the main changes between the Ludlovian, Downtonian, and Dittonian spore assemblages are not facies controlled. Three lines of evidence are considered important in this respect: (*a*) the nature of the spore record, (*b*) the Usk samples, and (*c*) comparisons with spore-pollen distribution patterns in modern sediments.

Nature of the spore record. A consideration of the spore record as a whole, and in particular the number of spore taxa through the Silurian and early Devonian, provides some evidence that the facies effects are slightly distorting a general evolutionary pattern.

TABLE 6. Total number of spore taxa (present paper) through the Silurian and early Lower Devonian. Upper Llandoverian record from Hoffmeister (1959)

	Genera	*Species, etc.*	*Sculptured forms*
Dittonian (Lower and Middle)	11	29	21
Downtonian	8	24	13
Ludlovian	6	15	6
Wenlockian	4	8	1
Upper Llandoverian	1	2	0

Most of these trilete spores probably represent the spores of land vascular plants although some algae produce spores in tetrads and bryophytes have trilete spores. No indisputable trilete spores have been found in pre-Silurian strata, and the earliest authenticated record of vascular plants is also from the Silurian. The spores gradually increase in variety through the Wenlock, Ludlow, Downtonian, and Dittonian

(Table 6) and some of this is clearly due to evolutionary changes rather than for instance distance from source areas and preservation factors.

The Usk samples. The evidence from the Silurian of Usk supports this general contention, for there although the relative abundance of spores is much greater than in the Silurian from other areas, the variety of spores is comparable with the Silurian assemblages from Ludlow and Millichope where spores form less than 1% of the spore/microplankton assemblages.

Comparison with palynological studies of recent sediments. Work on modern spore distribution patterns in clastic sediments shows that to a certain extent they reflect plant distribution (Muller 1959, Hopping 1967) and sedimentary distribution patterns, since water rather than wind is the dominant transporting agent (Muller 1959, Tschudy 1964, Groot *et al.* 1966, Groot 1966, Traverse and Ginsburg 1966, 1967). Consequently spore distribution patterns in the late Silurian and early Devonian are likely also to reflect these factors although clearly the plants were very different and nothing is known of their ecology. The only vascular plants known were very small (fragmentary axes of *Cooksonia* up to 6·5 cm.; Obrhel 1962) free-sporing pteridophytes. However, most of the differences in spore species between the Ludlovian, Downtonian, and Dittonian do not seem to be explicable on the basis of ecological or other contemporaneous factors. This is suggested by comparisons between data from the present study and samples from comparable environments on the Orinoco delta (Muller 1959), summarized in Table 7. They show that in spite of differences there is a much greater similarity between the contemporaneous pollen assemblages from various environments of the Orinoco region than between those from comparable environments in the Silurian–Devonian of the Welsh Borderland. This can clearly be seen from the comparisons in the species which are common to other environments. In all cases there are many more species which are common to other environments in the Recent sediments than within the sequence of the Welsh Borderland.

However, certain resemblances include the paucity of spore species in holomarine environments from the Orinoco delta and in the Ludlovian. In the latter this is doubtless related partly to evolutionary factors, but that it is partly due to spore distribution factors can be seen from the fact that certain spore species, e.g. cf. *Streelispora granulata* sp. nov. and *Apiculiretusispora synorea* sp. nov. have a rather sporadic distribution and also because Upper Ludlovian assemblages are less varied than assemblages from above and below. Further, this paucity of spore species in the Upper Ludlovian does not appear to be related to post-depositional preservation factors since many of the Upper Ludlovian rocks examined contain beautifully preserved microplankton.

COMPARISONS BETWEEN SOUTH WALES AND THE WELSH BORDERLAND

Ludlovian. The best spore assemblage found was in the Upper Cwm Clyd Beds (Sawdde Gorge), included *R.* cf. *warringtonii* sp. nov., *A. chulus* vars. *inframurinatus* var. nov., *chulus* var. nov., and *nanus*, var. nov., *Amb.* cf. *dilutus* (Hoffmeister) comb. nov., and *Retusotriletes* sp. The specimens of var. *inframurinatus* have very thick inframuri and resemble forms in the Bringewood and Lower Leintwardine Beds. Further *Amb.* cf.

dilutus has not been recognized with certainty above this horizon. These findings agree with previous suggestions of a Lower Leintwardine age for these beds (Potter and Price 1965) but cannot at this stage be regarded as proof of such an age. The assemblage contains abundant acritarchs and chitinozoans which have yet to be studied. The relative abundance of the spores is interesting for as at Usk there is no greater variety than at comparable Ludlovian levels.

TABLE 7. Comparisons between spore data from the Welsh Borderland with that from comparable environments in Recent deposits from the Orinoco Delta (Muller 1959)

Orinoco Delta			*Silurian/Devonian*
Holomarine	85%	22%	Ludlovian
Near shore (but not opposite river mouths)	43%	13%	Downtonian
Fluvio-marine	48%		
Delta (channel)	45%	11%	Dittonian
Delta (mud flats, lagoons)	45%		

(*a*) Percentage of species present which are common to all other deposits in the Orinoco Delta and the Silurian/Devonian respectively.

Near shore	48%	26%	Downtonian
Fluvio-marine	52%		
Delta (channel)	50%	11%	Dittonian
Delta (mud flats, lagoons)	50%		

(*b*) Percentage of species present which are common to holomarine and Ludlovian environments respectively.

Holomarine	85–92%	67%	Ludlovian
Delta (channel)	77%	37%	Dittonian
Delta (mud flats, lagoons)	77–82%		

(*c*) Percentage of species present which are common to near-shore and fluvio-marine environments and Downtonian environments respectively.

Holomarine	85%	22%	Ludlovian
Near-shore marine	74%	43%	Downtonian
Fluviomarine	70%		

(*d*) Percentage of species present which are common to Delta channel, mud flats and lagoons and Dittonian environments respectively.

Long Quarry Beds. The assemblages are poorly preserved but in Capel Horeb Quarry (Cwm Dwr region) a number of samples have yielded spores, acritarchs and chitinozoans; the spores are not abundant. Nevertheless no spore indicative of the Downtonian has so far been found. Specifically identified spores *R*. cf. *warringtonii*, *A*. *chulus* vars. *chulus* and *inframurinatus*, are long ranging, but indicate the possibility of a Ludlovian age.

Red Marl Group. So far the only assemblage obtained from these beds is from exposures at Freshwater East (north side of the bay). Samples from the ?Ludlovian contain abundant chitinozoa and acritarchs and relatively few spores belonging to the following species *A. chulus* var. *chulus*, *R.* cf. *warringtonii* and spores tentatively assigned to *Ambitisporites* cf. *dilutus*. In contrast the overlying Red Marl Group has yielded an assemblage including several typical Downtonian forms, e.g. *Synorisporites verrucatus* sp. nov. and *S. tripapillatus* sp. nov., which are abundant in all Downtonian samples from the Welsh Borderland. In addition *Archaeozonotriletes* cf. *divellomedium* Chibrickova 1959, *Perotrilites* sp. A, *Apiculiretusispora synorea* sp. nov. *Emphanisporites micrornatus* sp. nov. and *A. chulus* var. *chulus* occur. This assemblage suggests a Downtonian age.

Senni Beds. No assemblages equivalent to the distinctive Middle Dittonian assemblage have been seen in South Wales but a detailed study is in progress on the Breconian and the results will be published elsewhere. The best Senni Beds assemblages have been obtained from quarries at Storey Arms and Llanover (see also Mortimer 1967), and they contain a number of spore species which also occur in the Middle Dittonian. *Retusotriletes warringtonii*, *R.* cf. *minor* Kedo 1963, *R.* cf. *triangulatus* Streel 1967, *Streelispora newportensis* (Chaloner and Streel) comb. nov., *Chelinospora cassicula* sp. nov., *Archaeozonotriletes chulus* var. *chulus*, and *Emphanisporites micrornatus* sp. nov. Most of these are confined to the Llanover assemblages but both assemblages contain several forms which have not been found at lower horizons: *Apiculiretusispora* cf. *plicata* (Allen) Streel 1967, *Dibolisporites* cf. *Apiculiretusispora brandtii* Streel 1964, *Emphanisporites decoratus* Allen 1965, *E.* cf. *rotatus*, and *E.* cf. *robustus* McGregor 1961, *Retusotriletes* cf. *frivolus* var. *limbatus* Chibrickova 1959, other *Apiculiretusispora* and *Retusotriletes* spp. and *Dictyotriletes* sp. not seen in the lower assemblages.

These assemblages are strikingly similar in many respects to assemblages from the Carmyllie Beds ('Dittonian', Midland Valley of Scotland) which also contain robust ribbed *Emphanisporites*, the relatively large spores (*c.* 80 μ) *Dibolisporites* cf. *brandtii*, and the distinctive *Retusotriletes* cf. *frivolus* var. *limbatus*. In the Midland Valley this assemblage is overlain by one which contains annulate species of *Emphanisporites* (spp. *annulatus-erraticus*) and relatively large zonate-pseudosaccate forms (Richardson 1967). So far neither of the latter has been found in the Senni Beds but the species *E. annulatus* McGregor 1961 and possible *E. erraticus* (Eisenack) McGregor 1961 occur in strata of Senni-like lithology in the Witney borehole (Chaloner 1963, Richardson 1967).

PREVIOUS WORK AND COMPARISON WITH OTHER AREAS

Wenlock–Ludlow. Hoffmeister (1959), Downie (1963) have recorded trilete spores from the Silurian, and Cramer (1966) from near the Ludlovian–Gedinnian boundary. In total these records are consistent with a poorly developed, but nevertheless distinctive, spore flora in the Silurian. This lack of variety does not suggest a long pre-Silurian history for trilete spores and although supposed trilete spores have been recorded from the Ordovician (Taugourdeau 1965) and older strata (Naumova 1953), they are either too poorly preserved to be certain of their nature or clearly lack haptotypic features and are therefore more properly assignable to the acritarchs.

Hoffmeister (1959) described an assemblage from a borehole in Libya dated by graptolites as belonging to 'high Lower Silurian'. The assemblage, represented by two closely similar spore species *Ambitisporites avitus* and *A.* cf. *dilutus*, probably constitutes the oldest trilete spores in the geological record. Downie (1963) found similar spores (*A.* cf. *dilutus*) in the Wenlock Shale of the Welsh Borderland, and also a single specimen with verrucate sculpture (*Lophotriletes*). These spores are all, with a single exception, smooth-walled with a tendency to thicken in the equatorial region. Cramer's (1966) assemblage from León, Spain shows more variety than those described by Hoffmeister and Downie, for, in addition to forms similar to *A. avitus* and *A.* cf. *dilutus* (pl. 2, fig. 15), other smooth-walled spores with a distinctive proximal thinning (*Archaeozonotriletes chulus*), and spores with apiculate sculpture, occur. Other palynomorphs doubtfully referred to as spores have verrucate to reticulate sculpture.

The Wenlock Shale contains smooth-walled trilete spores some of which are closely similar to those previously recorded by Hoffmeister and Downie but here they are referred to a single genus *Ambitisporites* e.g. *A. dilutus*, *A.* cf. *dilutus*, and *A.* cf. *avitus*. In addition other smooth-walled spores, *Retusotriletes* cf. *warringtonii* and atypical representatives of *Archaeozonotriletes chulus* var. *nanus*, were recorded. The Wenlock Limestone assemblage is similar but contains rare verrucate spores and in the Ludlovian there is an increasing diversity of sculptured spores which are, however, still rare. Spores from the Upper Ludlow are comparable to Cramer's assemblage from Spain with *Archaeozonotriletes chulus*, and species of *Apiculiretusispora* although forms comparable to Cramer's species have not been found.

Downtonian. Nothing comparable with the distinctive Lower Downtonian spore assemblages has been described from elsewhere. However, Allen (1965, 1967) in his description of Lower and Middle Devonian spore assemblages from Vestspitsbergen records an assemblage from the Red Bay Group of Fraenkelryggen, 'a probable equivalent to the Upper Downtonian and Dittonian in the Anglo-Welsh area'. These spores are poorly preserved and not figured, but the presence of *E. minutus* Allen 1965 (similar to *E.* cf. *neglectus*) in both the Spitsbergen and the Welsh Borderland samples may be significant. Only rare specimens of this species with poorly developed ribs have so far been found in the Downtonian whereas it occurs in the '*Psammosteus*' Limestone Group and the Middle Ditton Group, in the latter with other fine-ribbed *Emphanisporites*, many of which have distal sculpture. This situation is broadly comparable with that described for Spitsbergen where at higher horizons and in the Wood Bay Formation (Austfjorden Sandstone Member) Allen records *E. minutus* and *E. neglectus* Vigran 1964, with *E. decoratus* Allen 1965 which has distal sculpture. However, this assemblage contains more complex forms, e.g. poorly preserved ?zonate *Cirratriradites dissutus* Allen 1965 and in the megaspore size range *Trileites oxfordiensis* Chaloner 1963; such types have not so far been found in the Dittonian where all the spores, with one possible exception, are of small size. The exception is a spinose body (? spore) which has so far only been found in a fragmentary condition.

In general, although there have been relatively few areas studied in detail, these show a similar pattern of Late Silurian and Early Devonian spore assemblages to that observed in the Welsh Borderland. However, later Lower Devonian spore assemblages, e.g. those described by Moreau-Benoit (1966, 1967) from the Siegenian to Emsian have much more varied composition than those from strata of apparently equivalent age in Belgium (Streel 1967).

Botanical significance. Chaloner (1967) commented on the spore evidence in relation to land plant evolution when only a few Silurian samples had yielded clear trilete spores. However, in spite of the number of Ludlovian samples investigated the overall trend of spore diversification has not been substantially altered. Table 6 shows a gradual increase in spore genera and species which appears to be evolutionary, and although comparison with Muller's work suggests less spore variety in holomarine sediments, the trend is consistent and repeated in Spain (Cramer 1966) and Gaspé (McGregor 1967). Within the Silurian and Lowermost Devonian spores are dominantly azonate or with only small equatorial thickenings (Richardson 1967). Forms with proximal radial ribs are at first apparently absent (Silurian) then poorly developed (Downtonian) then diverse and later robust (Dittonian–Breconian). Surely these changes reflect contemporaneous land plant evolution in the Silurian and Lower Devonian.

More specifically the gradual morphological changes in spores of the *Ambitisporites-Archaeozonotriletes* complex through the Wenlock and Ludlow seem to suggest an evolutionary cause, and the size of the spores in the present study confirms earlier work (Chaloner 1967, Richardson 1967) in suggesting that the plants producing them were all homosporous.

Although it is probable that most of the spores studied are of land vascular plants there is unfortunately no direct evidence of this. The spores of *Cooksonia* (the only vascular plant known in the Silurian and Downtonian) have not yet been described in detail or clearly illustrated. However, many of the spores found in these rocks have very thick walls which are more typical of land plants (bryophytes and pteridophytes) than of algae, and one such thick-walled species, *Archaeozonotriletes chulus*, occurs in considerable numbers in fluviatile Dittonian sediments as well as marine strata and thus most probably originated from a land plant.

SYSTEMATIC DESCRIPTIONS

All slides with the prefix WB are in the Department of Geology, King's College, London; instrument settings of Zeiss microscope 400349. Figured specimens bearing the index letters MPK are stored in the Institute of Geological Sciences, Leeds.

Terminology used is that proposed by Potonié and Kremp (1954) with modifications proposed by the International Commission for Palaeozoic Microfloras (Couper and Grebe, Krefeld 1961, and Grebe, in preparation) and in addition the term 'Biform sculpture' (Richardson 1965); and the term 'perine' to include perine-like layers which may not be homologous with the perine of modern spores.

Genera and species described below are considered as form genera and species based purely on arbitrary morphological criteria.

Anteturma SPORITES H. Potonié 1893
Turma TRILETES Reinsch 1891
Subturma AZONOTRILETES Luber 1935
Infraturma LAEVIGATI (Bennie and Kidston) Potonié and Kremp 1954
Genus RETUSOTRILETES (Naumova) Richardson 1965 non Streel 1964

Type species. R. pychovii Naumova 1953 (lectotype species of Richardson 1965).

Discussion. Two emendations of the Genus *Retusotriletes* have been proposed. Richardson (1965) published an emendation proposing *R. pychovii* Naumova (1953, pl. 4, fig. 5) as the type species. While this paper was in press Streel (1964) also published an emendation of the same genus but following Potonié in using *R. simplex* Naumova as the type species. Potonié used an arbitrary procedure in selecting the first species of the genus described by Naumova (see Lanjouw *et al.*, 1961, p. 65, para. 4). Examination of Naumova's illustrations (pl. 2, fig. 9, and pl. 15, fig. 14) shows that *R. simplex* has curvaturae imperfectae and no contact area differentiation and thus lacks the diagnostic characters of the genus. On the other hand *R. pychovii* has clearly defined contact areas, emphasized in Naumova's description of this species (but not in the description for *R. simplex*). Consequently *R. pychovii* is preferred, although this must be regarded as provisional until Naumova's type and co-type material is re-examined.

Retusotriletes dittonensis sp. nov.

Plate 37, figs. 1, 2

Holotype. Size 41 × 54 μ; slide WB 125, ref. 3141033. Ditton Group, Dairy Dingle, Gedinnian.

Occurrence. As above.

Diagnosis. Curvaturae perfectae well developed, contact areas slightly depressed; exine of variable thickness, with the greatest thickness distally.

Description. Size range 35–57 μ (30 specimens measured), mode 48 μ. Amb circular, in equatorial view hemispherical with flattened to slightly concave contact areas, exine outside the contact area appears raised. Exine distally thicker than proximally, distally 4–6·5 μ, equatorially 2–4 μ (maximum observed variation on a single specimen, equatorial width 2·5, distal 6·5). Contact areas distinct, about $\frac{2}{3}$–$\frac{3}{4}$ spore radius, on some specimens one contact area appears larger than the other two, occasionally apical region darker, curvaturae perfectae form narrow ridges 0·5 μ wide, contact faces shagrinate to faintly striate, or slightly infragranular, exine outside contact areas homogeneous. Triradiate mark distinct, sutures $\frac{3}{5}$–$\frac{3}{4}$ spore radius, occasionally accompanied by low lips.

Comparison and remarks. R. pychovii Naumova 1953 has a similar size range, 40–50 μ, distinct curvaturae perfectae, and a relatively thick wall, but it is not possible to see from Naumova's drawings whether the exine is thickened distally. Almost identical spores occur in the same assemblage which have a distinct, fine, radiating muri on the contact areas (compare *Emphanisporites* sp. A). Similar specimens occur in the Downtonian but have a thinner distal exine and curvaturae which coincide with the equator at their maximum extent; in polar compression the wall at the equator appears to be of greater thickness in the interradial areas due to the coincidence of the curvaturae with the equator.

Retusotriletes dubius (Eisenack) Richardson 1965

Plate 38, figs. 1–2

Occurrence. Lower Downtonian, Linton Quarry, and Downton Gorge. Relatively rare.

Remarks. The Downtonian specimens are 56–64 μ (5 specimens measured). In common with Eisenack's specimens and the Scottish Middle Devonian material they are triangular in outline, have curvaturae which coincide with the equator and give the appearance of thickened interradial areas, and have a darkened apical area.

Retusotriletes warringtonii sp. nov.

Plate 37, figs. 7–8

Holotype. Size 24 × 28 μ; slide 135, ref. 386994, Ditton Group, Dairy Dingle; Gedinnian.

Occurrence. Lower Downtonian and Dittonian.

Diagnosis. Small triangular to subtriangular laevigate spores with curvaturae perfectae that coincide with equator for most of their length.

Description. Size range 18–36 μ (20 specimens measured). Amb sub-triangular to distinctly triangular. Exine smooth homogeneous relatively thick 1·5–2 μ. Contact areas demarcated equatorially by curvaturae perfectae which usually coincide with the equator, only seen clearly in tipped specimens. Triradiate mark nearly equals spore radius accompanied by lips which taper from the pole towards the equator, maximum height of the lips 1–2 μ.

Comparison. Differs from *R*. cf. *minor* by its distinct sub-triangular to triangular equatorial outline.

Retusotriletes cf. *warringtonii* sp. nov.

Plate 37, figs. 9–11

Occurrence. Wenlock, Ludlow, and Lower Downtonian.

Description. Size range 22–32 μ (13 specimens measured). Exine homogeneous. Amb subtriangular to triangular, relatively thin and frequently folded. Contact areas coincide with the proximal face except in the interradial areas. Curvaturae perfectae coincide with the equator, only seen clearly in slightly tipped specimens. Triradiate mark nearly equals spore radius, accompanied by lips.

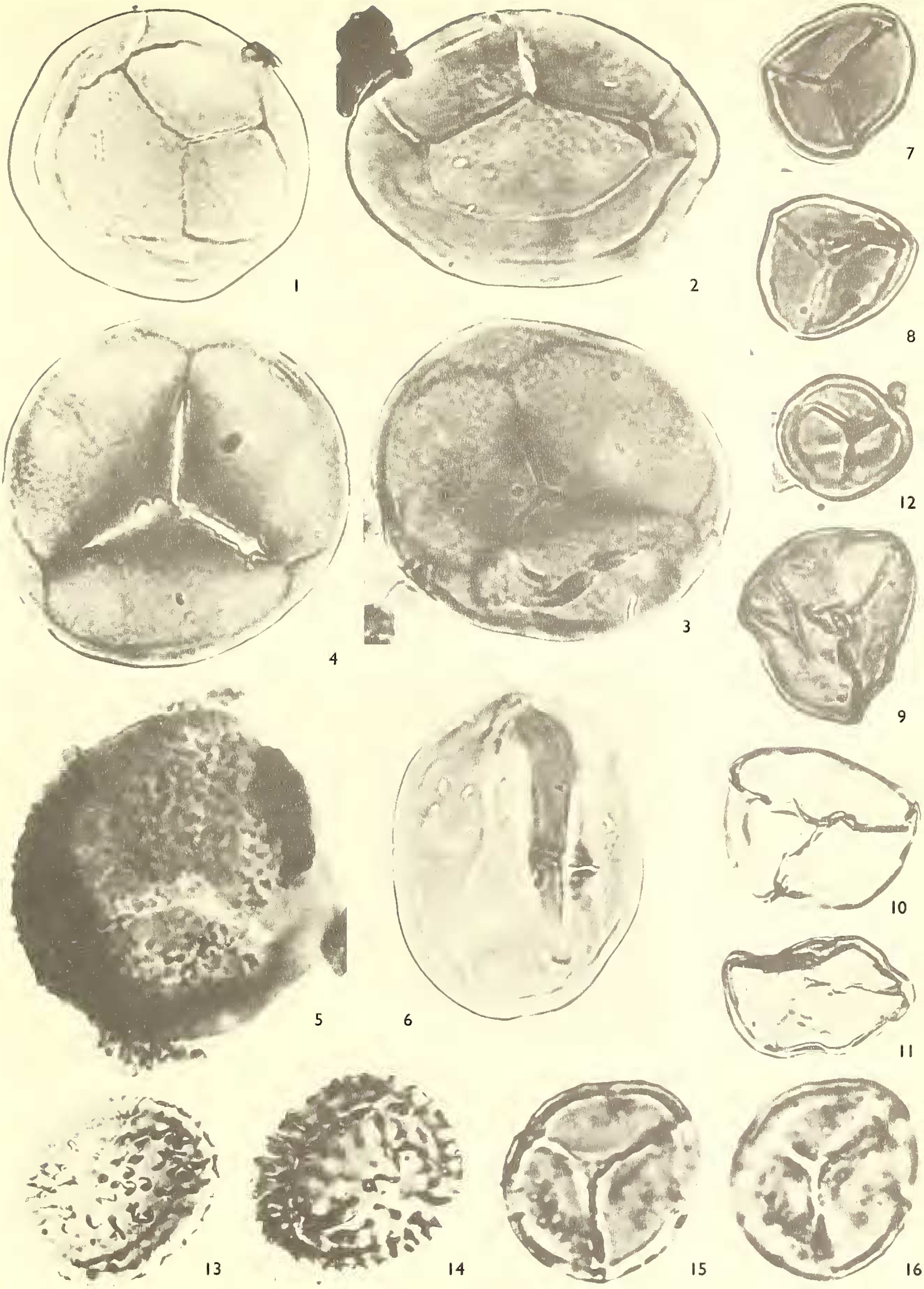
Comparison. In size similar to *Retusotriletes* cf. *minor* and *R*. *warringtonii* but differs in having a thinner crumpled exine.

EXPLANATION OF PLATE 37

All figures × 1,000 except where stated otherwise.

Figs. 1–12. *Retusotriletes* spp. 1–2. *R. dittonensis* sp. nov. 1, Holotype; unequal development of contact areas. 2, Lateral compression showing thick exine over distal surface; WB 127/417959, Ditton Group. 3–5. *R.* cf. *triargulatus* (Streel) Streel 1967; Ditton Group. 3, Showing apical triangular thickening with thinner apical area; WB 125/3601053. 4, With uniformly thickened apical area; WB 128/451921. 5, Showing disintegrating outer sculptured layer; WB 135/410932. 6, *R.* sp. A, Lateral compression showing curvaturae perfectae; Downton Castle Sandstone Group, WB 37/4041018. 7–8. *R. warringtonii* sp. nov. 7, Holotype. 8, Tipped specimen showing curvaturae perfectae; Ditton Group. WB 135/282982. 9–11. *R.* cf. *warringtonii* sp. nov. 9, Thick-walled specimen, Lower Elton Beds, MPK 15. 10, Thin-walled specimen, Lower Elton Beds, MPK 8. 11, Lower Whitcliffe Beds, MPK 15. 12, *R.* cf. *minor* Kedo 1963; Ditton Group, WB 135/4261000.

Figs. 13–16. *Apiculiretusispora* spp. 13–14. *Apiculiretusispora cherata* sp. nov.; holotype. 13, Distal focus. 14, proximal focus showing smooth contact areas and Y-folds. 15–16. *A. microconus* sp. nov.; holotype, × 2,000. 15, Proximal focus showing lips. 16, Distal focus showing sparse minute coni.



RICHARDSON and LISTER, Silurian and Devonian miospores

Retusotriletes cf. *minor* Kedo 1963

Plate 37, fig. 12

Occurrence. Lower Downtonian and Dittonian.

Description. Size range 14–36 μ (40 specimens measured) mode 28 μ. Amb circular to triangular with convex sides and rounded apices. Spores usually preserved in polar compression. Exine 0·5–1·5 μ thick, smooth and homogeneous. Contact areas frequently slightly depressed, occasional specimens show a thinner area at the proximal pole; triradiate lips 0·5–2 μ high, $\frac{5}{6}$ to nearly equal spore radius, lips merge into curvaturae perfectae which sometimes coincide with the equatorial outline; lips occasionally thickened where they pass into the curvaturae.

Comparison and remarks. In size these spores compare with *Retusotriletes minor* Kedo 1963 (26–30 μ), however the latter lacks lips. '*R.*' *simplex* Naumova 1953 is also small (30–5 μ) but lacks lips and has curvaturae imperfectae.

Retusotriletes cf. (al. *Phyllothecotriletes*) *triangulatus* (Streel) Streel 1967

Plate 37, figs. 3–5; text-fig. 3.

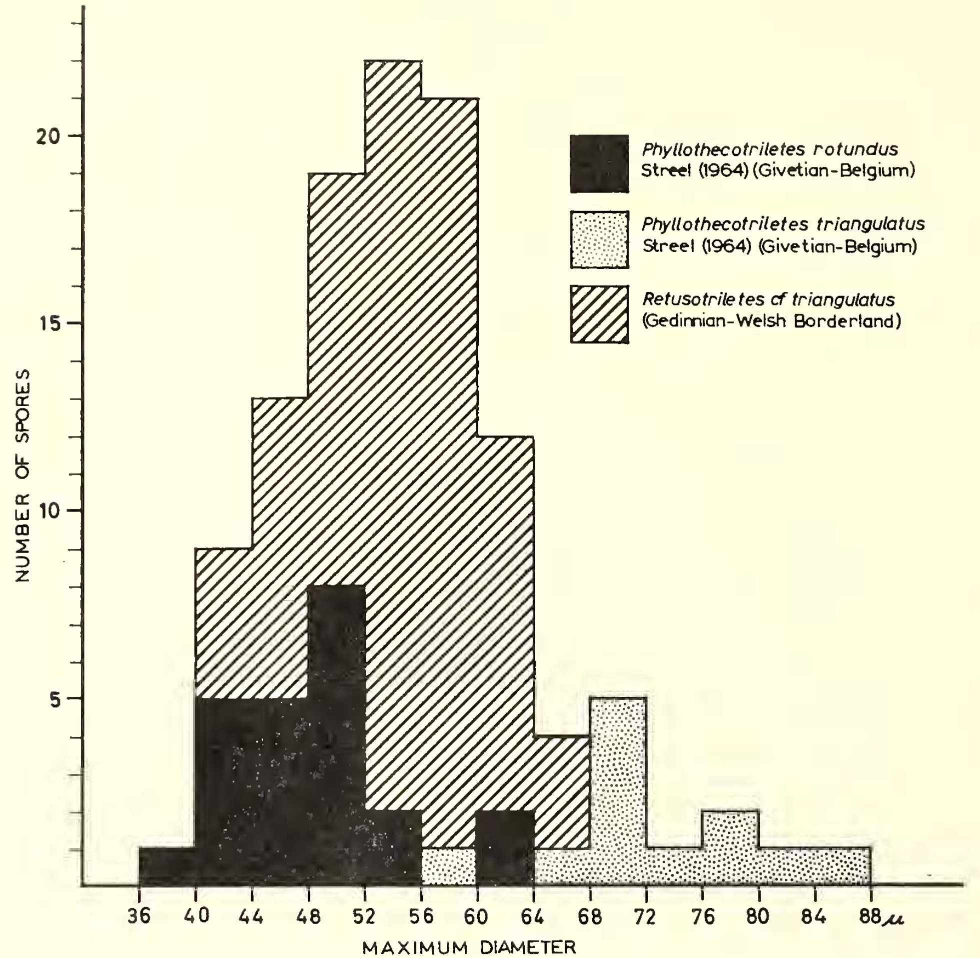
cf. 1964 *Phyllothecotriletes triangulatus* Streel

Occurrence. Ditton Group, Dairy Dingle, Gedinnian; relatively common.

Description. Size range 41–68 μ (100 specimens measured), mode 58 μ. Amb circular to subcircular. Spores usually preserved in polar compression or slightly oblique. Exine typically 2 μ thick, externally smooth. Contact areas delimited by distinct curvaturae which usually follow the equatorial margin except in the radial areas in polar compression. Triradiate mark surrounded by a thickened triangular area in the apical region, areas inside and outside the triangular area less dense, in some specimens triangular area of uniform density; triangle with straight to slightly convex or concave sides, sutures within the triangle distinct, about $\frac{1}{2}$ radius, frequently splayed open, continued as dark lines to the curvaturae, total length of triradiate mark $\frac{2}{3}$–$\frac{5}{6}$ radius.

Comparison. Several spore species have a thickened triangular apical area and some have, in addition, curvaturae perfectae. Three species of the latter type resemble the spores described above; these are '*Calamospora*' *witneyana* Chaloner 1963, *Phyllothecotriletes rotundus* and *P. triangulatus* (Streel 1964). *C. witneyana* is much larger (110–96 μ) and has a mean of 165 μ. In size distribution the Dittonian specimens correspond closely to *P. rotundus* but in the nature of the apical region they are more similar to *P. triangulatus* since the apical thickening is basically triangular in shape. The apical thickening is sometimes less dense in the inner part and in some specimens this appears to be a secondary development.

Botanical affinities. Recently a probable coenopterid fern (*Dawsonites*) has been described from Gaspé (Banks, Hueber, and Leclerq 1964). The spores exines are two layered; the outer layer (? perispore) is sculptured but frequently separates from an inner smooth spore which has a darkened apical region and is closely similar to *R.* cf. *triangulatus*. In the Ditton Group of the Welsh Borderland occasional specimens show this outer layer still attached but the bulk of the specimens have lost it. Similar spores also occur in the 'Dittonian' (Carmyllie and Strathmore beds) of the Midland Valley but here many more of the specimens have retained the outer layer. McGregor and Owens (1966, pl. 2, figs. 18, 19) also figure similar specimens from the Battery Point Formation, lower part (Emsian), eastern Gaspé Peninsula, Quebec.



TEXT-FIG. 3. Size distribution of *Retusotriletes* cf. *triangulatus* (Streel) from the Dittonian of the Welsh Borderland compared with Streel's data from the Lower Givetian of Goé, Belgium (Streel 1964).

Retusotriletes sp. A

Plate 37, fig. 6

Occurrence. Upper Elton and Upper Whitcliffe Beds, Ludlovian; Lower Downtonian, Linton quarry, Ludford and Downton Gorge.

Description. Size range 30–68 μ (24 specimens measured). Amb subcircular. Exine homogeneous of variable thickness, equatorially 2–4 μ thick, thickest in the interradial areas, distally 3–3·5 μ. Contact areas coincide with the proximal face except in the inter-radial areas. Curvaturae only clearly seen in oblique compression as in polar view they merge with the equator. Triradiate mark distinct $\frac{4}{5}$ to nearly equal spore radius.

Comparison and remarks. Most of the specimens seen are distorted or poorly preserved and hence no specific assignment is made. However, they are clearly distinct from *R. dittonensis* in that the contact areas are not as distinct, curvaturae coincide with the equator, and though the exine is variably thickened, it is not as thick distally as in *R. dittonensis* sp. nov. Ludlovian specimens have a slightly thinner exine.

Infraturma APICULATI (Bennie and Kidston) Potonié 1956

Genus APICULIRETUSISPORA Streel 1964

Type species. A. brandtii Streel 1964

Apiculiretusispora cherata sp. nov.

Plate 37, figs. 13–14

Holotype. Size 31 × 38 μ, including spines, spine length 2–3 μ; slide WB 128, ref. 437941; Ditton Group, Dairy Dingle, Gedinnian.

Occurrence. As above.

Diagnosis. Exine relatively thick, sculpture spinose, elements have bulbous bases, slender stems, and dominantly blunt, occasionally spatulate apices; triradiate mark nearly equal to equal spore radius.

Description. Size 30–46 μ (120 specimens measured), mode 38 μ. Amb subcircular to subtriangular, distal hemisphere convex in lateral view. Exine 2–3 μ thick, typically 2·5 μ. Contact areas, distinct, smooth and infragranular(?) towards the pole, granular towards the equator; contact areas equal or nearly equal to spore radius. Exine outside the contact areas bears dominantly spinose sculpture, occasional cones also present, elements circular in plan, with broad bases, rapidly taper to slender parallel-sided or slightly tapered stems, spine apices dominantly flattened but occasionally pointed, sometimes distinctly spatulate; width of bases typically 1·5 μ, range 0·5–1·5 μ, stem width around 0·5 μ, spine length variable, 1–6 μ, range on a single specimen typically 3–3·5 μ; elements 1–2·5 μ apart. Triradiate mark nearly equal, to equal, spore radius, sutures sometimes accompanied by lips 1·5–2·5 μ high.

Comparison. '*Acanthotriletes*' *raptus* Allen 1965 is similar but has shorter Y-rays and more closely packed spines.

Apiculiretusispora microconus sp. nov.

Plate 37, figs. 15–16

Holotype. Size 16 × 19·5 μ; slide WB 135, ref. 356982; Ditton Group, Dairy Dingle, Gedinnian.

Occurrence. As above.

Diagnosis. Small spores with minute distal sculpture of barely discernible coni or grana to distinct coni.

Description. Size range 13–24 μ (60 specimens measured), mode 18 μ. Amb triangular with convex sides and rounded apices. Exine homogeneous 0·5–1 μ thick. Contact areas smooth bordered by curvaturae which nearly equal spore radius or merge with the equatorial outline. Exine equatorially and distally sculptured by minute, barely discernible, grana or coni, to distinct coni, up to 0·5 μ wide and 0·5 μ high, 1–2 μ apart. Triradiate mark distinct, sutures nearly equal to equal spore radius, sometimes accompanied by triradiate folds.

Comparison. The small size and minute sculpture distinguish this species from other species of *Apiculiretusispora*.

Apiculiretusispora spicula sp. nov.

Plate 38, figs. 3–4

Holotype. Size 35 × 40 μ; slide WB 62, ref. 3931022; Lower Downtonian, Linton Quarry.

Occurrence. Lower Downtonian, as above, Ludford and Downton Gorge.

Diagnosis. Contact areas distinct, sculpture consists of sparse, sharply pointed, slender cones or small spines.

Description. Size range 30–46 μ (34 specimens measured), mode 46 μ. Amb circular to subcircular. Exine 1–2 μ thick, typically 1·5 μ, at the equator slightly thicker distally. Contact areas distinct usually unequal in size, delimited by fine curvaturae perfectae, areas occasionally smooth, slightly granulose, or bear faint radial 'muroid folds' less than 1 μ wide, contact areas nearly equal to spore radius. Outside the contact areas exine covered by slender sharply pointed spines or cones, elements 0·5–1 μ wide, 1–2 μ high, height two to four times basal diameter; elements 1–3 μ apart. Triradiate mark distinct, sutures $\frac{1}{2}$–$\frac{3}{4}$ spore radius.

Comparison and remarks. The sparse slender cones and spines distinguish this species from other species described in the present paper. *A. brandtii* Streel 1964 is much larger. Specimens from Ludford frequently show very fine, barely discernible, proximal ribs.

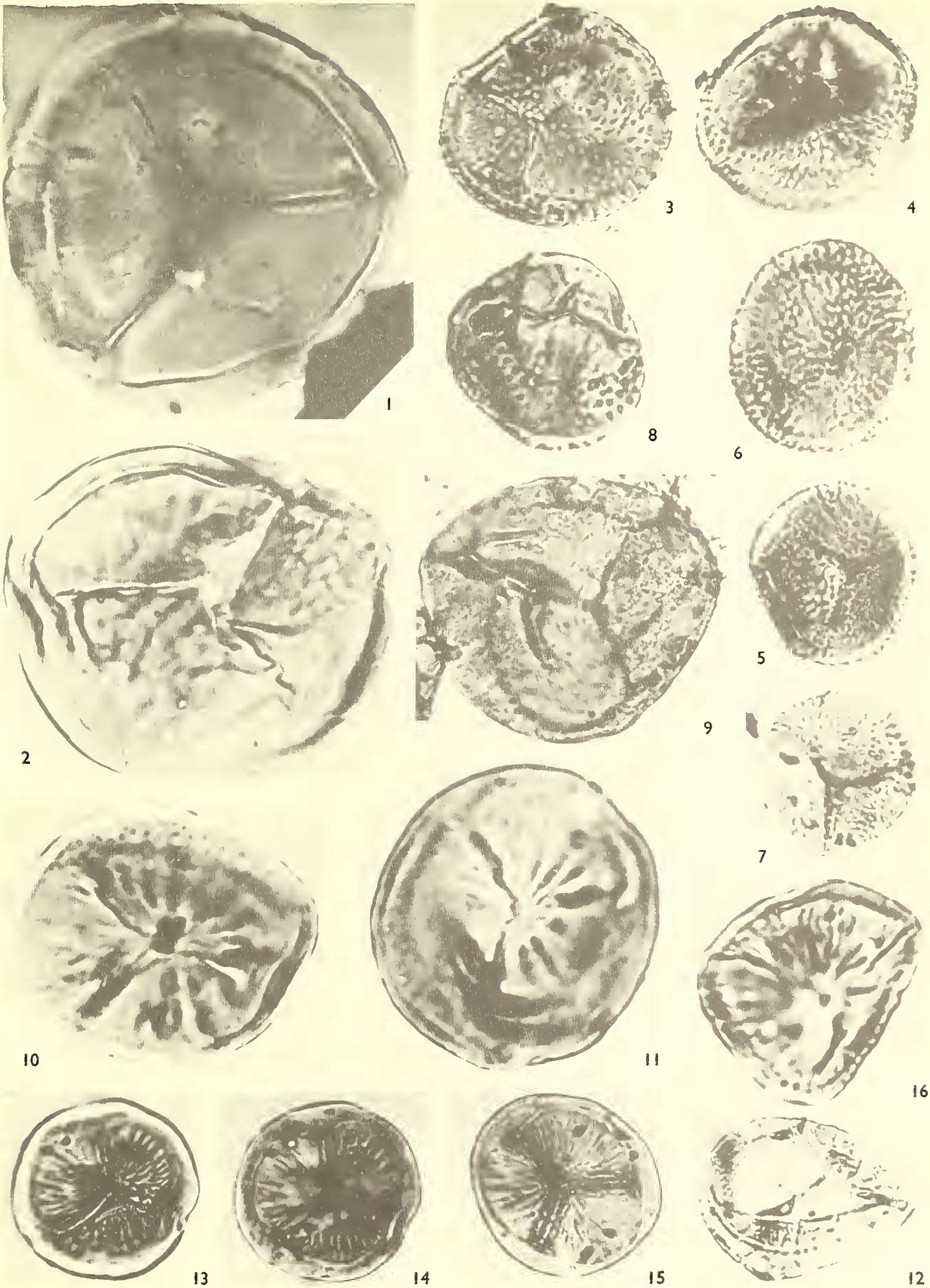
EXPLANATION OF PLATE 38

All figures × 1,000 except where stated otherwise.

Figs. 1–2. *Retusotriletes dubius* Richardson 1965; Downton Castle Sandstone Group. 1, Polar compression showing thickened apical area; WB 38/433949. 2, oblique compression showing curvaturae perfectae; WB 38/2831041.

Figs. 3–9. *Apiculiretusispora* spp. 3–4. *A spicula* sp. nov. 3, Holotype. 4, Showing depressed smooth contact areas; Downton Castle Sandstone Group, WB 32/4571042. 5–6. *A. synorea* sp. nov. 5, Holotype. 6, Showing wrinkling of contact areas; Downton Castle Sandstone Group, WB 32/341968. 7, *A.* sp. A; Downton Castle Sandstone Group, WB 64/371891. 8, *A.* sp. B; Ditton Group, WB 125/400891. 9, *A.* sp. C; Lower Whitcliffe Beds, MPK 40.

Figs. 10–16. *Emphanisporites* spp. 10–11. *E. micrornatus* sp. nov.; × 2,000. 10, Holotype, tipped specimen showing proximal radial ribs and distal sculpture. 11, Proximal polar view, Ditton Group, WB 127/347879. 12, *E.* cf. *micrornatus* sp. nov.; Downton Castle Sandstone Group, WB 54/426930. 13–15. *E. epicautus* sp. nov. 13–14, Holotype. 13, Showing apical thickening. 14, Showing well-marked contact areas. 15, Specimen showing thickenings at ends of Y-rays; Ditton Group, WB 139/363911. 16, *E.* cf. *neglectus* Vigran; specimen showing fine radial ribs and curvaturae that coincide with equator, × 2,000; Ditton Group, WB 134/363910.



RICHARDSON and LISTER, Silurian and Devonian miospores

Apiculiretusispora synorea sp. nov.

Plate 38, figs. 5–6

Holotype. Size 29×31·5 μ; slide WB 32, ref. 4531084; Lower Downtonian, Linton Quarry, Gedinnian.

Occurrence. Upper Elton Beds, Ludlovian and Lower Downtonian.

Diagnosis. Contact areas distinctly wrinkled, bulge prominently in the interradial areas; sculpture consists of stout, densely packed cones.

Description. Size range 26–43 μ (80 specimens measured), mode 33 μ. Amb circular to subcircular. Exine 2 μ at the equator, 3 μ at the distal pole. Contact areas distinct, more or less $\frac{1}{2}$ the radius in the radial area, swell to nearly equal to the radius in the interradial region, exine in the contact areas wrinkled into fine irregular folds. Exine outside the contact areas sculptured, sculptural elements consist of stout cones, cones more or less isodiametric, 0·5–1·5 μ, elements closely packed 0·5–1 μ apart, rounded in plan, in profile may be uniformly tapered, or have rapidly tapered bases surmounted by slender pointed stems, occasional elements become distinctly biform but this does not form a constant character. Triradiate mark $\frac{1}{2}$–$\frac{3}{5}$ spore radius, accompanied by broad convolute lips.

Comparison. The coarse, closely packed cones and bulging contact areas distinguish this species from *A. spicula* sp. nov. *A. brandtii* Streel 1964 is much larger and has more sparse sculpture.

Apiculiretusispora sp. A

Plate 38, fig. 7

Occurrence. Lower Downtonian, Linton Quarry, Ludford, and Downton Gorge.

Description. Size range 22–32 μ (11 specimens measured). Amb triangular with convex sides and rounded apices. Proximal face smooth or covered with fine radial muroid folds, exine distally covered by short pointed spines, 0·5–1 μ wide, 1–2 μ high, elements closely packed. Triradiate mark accompanied by large folds, 1·5–2 μ high, equal spore radius.

Comparison. The sculpture of these specimens is very similar to that of *A. synorea* sp. nov.; however type A is distinctly triangular and has prominent lips which reach the equator.

Apiculiretusispora sp. B

Plate 38, fig. 8

Occurrence. Downtonian, Gorsley Common, and Long Mountain, Ditton Group, Dairy Dingle.

Description. Size range 21–8 μ (10 specimens measured). Amb subtriangular, frequently preserved in lateral compression. Contact areas bounded by distinct curvaturae, contact face smooth. Exine homogeneous 1 μ thick proximally, 1–2 μ thick at the equator and distally. Exine outside the contact areas covered by distinct coni, with broad bases, and rounded to pointed apices, width 0·5–2 μ, typically 1 μ, height 0·5–1 μ typically less than 0·5 μ, elements 0·5–1·5 μ apart. Triradiate mark ⅔ radius accompanied by lips 1 μ wide.

Comparison. Distinguished from *Apiculiretusispora* sp. A by broad, low coni, and distinct curvaturae.

Apiculiretusispora sp. C

Plate 38, fig. 9

Occurrence. Upper Ludlovian and Lower Downtonian, Ludlow and Gorsley Common. Rare.

Description. Size range 40–50 μ (4 specimens measured). Amb subcircular to subtriangular, contact areas distinct delimited by thickened curvaturae perfectae, equal or nearly equal spore radius. Except for contact areas which are smooth, exine covered by minute closely packed sculptural elements, 0·5 μ or less, more or less equidimensional. Triradiate mark nearly equal to the spore radius accompanied by folds.

Remarks. These specimens are closely similar to those of *Emphanisporites* cf. *micrornatus* sp. nov. except that they lack proximal radial ribs and tend to be larger.

Infraturma MURORNATI Potonié and Kremp 1954
Genus EMPHANISPORITES McGregor 1961

Type species. Emphanisporites rotatus McGregor 1961.

Emphanisporites micrornatus sp. nov.

Plate 38, figs. 10–11

Holotype. Size 21×24 μ; slide WB 133, ref. 4161025; Ditton Group, Dairy Dingle, Gedinnian.

Occurrence. As above.

Diagnosis. Spores small with distinct curvaturae, relatively robust proximal radial muri, and minute distal sculpture of coni to grana.

Description. Size range 19–38 μ (100 specimens measured), mode 28 μ. Amb circular to subcircular, spores originally subspherical with flattened proximal pole, frequently preserved in oblique compression. Exine 1–1·5 μ thick; proximal face with distinct curvaturae perfectae, slightly thickened, contact areas slightly less than, or equal to, spore radius, ornamented with 5–7 radially arranged muri, which are relatively robust, only slightly tapering, and 1–2·5 μ wide. Distal hemisphere sculptured by sparse minute coni to grana less than 0·5 μ high. Triradiate mark accompanied by folds ¾ to nearly equal spore radius.

Comparison. The minute distal sculpture of *E. micrornatus* sp. nov. distinguishes this species from *E. decoratus* Allen 1965 which has clearly discernible and relatively large cones or spines and from *E. neglectus* Vigran 1964 which is also distinctly subtriangular, and smaller (Vigran's size range is 9·5–17 μ). Spores placed by Allen (1965) in the latter species occasionally have fine granules and the figured specimen is closely similar to *E. micrornatus* sp. nov. In *E. spinaeformis* Schultz (in Lanninger 1968), the proximal muri are thicker and converge on the trilete sutures forming a 'herring-bone' pattern ('fischgratenartige').

Remarks. The sparse minute sculpture can frequently only be seen under high magnifications and could easily be overlooked.

Emphanisporites cf. *micrornatus* sp. nov.

Plate 38, fig. 12

Occurrence. Downtonian, Linton Quarry and Wallop Hall Quarry, Long Mountain.

Description. Size 24–41 μ (11 specimens measured). Ambsubcircular to subtriangular, contact areas distinct, delimited by thickened curvaturae perfectae; contact areas equal to spore radius, bear radial muri, muri 1–1·5 μ wide, rather indistinct, gradually tapering. Distal surface bears sculpture of small rounded coni or grana, rounded in profile, more or less equidimensional, 0·5 μ or less, number of muri 7–10 per area. Triradiate mark nearly equal to equal radius accompanied by folds.

Comparison. These spores are similar to *E. micrornatus* sp. nov. in having fine sculpture, but the sculptural elements are more densely packed and the spore exine is much thinner and crumpled into taper pointed folds. Somewhat larger spores lacking the fine proximal ribs but which are otherwise identical occur rarely in the Upper Ludlow and the Lower Downtonian; they are referred to as *Apiculiretusispora* sp. C. Size range 40–50 μ (4 specimens).

Emphanisporites epicautus sp. nov.

Plate 38, figs. 13–15

Holotype. Size 30 × 30 μ; slide WB 135, ref. 3931030; Ditton Group, Dairy Dingle, Gedinnian.

Occurrence. As above.

Diagnosis. Spores small with distinct curvaturae perfectae and contact areas, fine proximal radial muri and thickened apical area; distally laevigate.

Description. Size range 25–40 μ (55 specimens measured), mode 32 μ. Amb subcircular to subtriangular. Spores originally more or less hemispherical. Exine homogeneous 1–2 μ thick. Distal hemisphere smooth. Proximal face with well marked contact areas bounded by distinct curvaturae perfectae, contact areas $\frac{4}{5}$ to equal spore radius; each contact area has 7–10 radiating muri which are 0·5 μ high and have a maximum width of 0·5–1·5 μ but taper sharply towards spore apex where some of them become fused together, muri cover about $\frac{5}{6}$ of the radius of the contact area. Spore apex has a distinct triangular thickened area which extends along the Y-rays for $\frac{1}{4}$–$\frac{1}{2}$ their length. Triradiate mark distinct, sutures $\frac{2}{3}$ to nearly equal spore radius.

Remarks. Naumova (1953) figured but did not describe *Stenozonotriletes ornatissimus*; Chibrikova (1959) gave a description in which she recorded that *S. ornatissimus* had proximal radial 'striations', a size range of 35–40 μ, and also a proximal apical triangular thickening in some specimens. No other species of *Emphanisporites* has the latter feature and *E. epicautus* sp. nov. differs from *S. ornatissimus* (Naum.) ex Chibrickova since it has well developed contact areas, the three semicircular areas are clearly seen in polar compression (Pl. 38, figs. 14 and 15). *Retusotriletes actinomorphus* Chibrickova 1962 has curvaturae perfectae and well-developed contact areas but lacks the apical thickening.

Emphanisporites cf. *neglectus* Vigran 1964

Plate 38, fig. 16

Occurrence. Lower Downtonian, Dittonian.

Description. Size range 18–24 μ (16 specimens measured). Amb triangular to subtriangular; proximal face slightly concave, appears to be thinner than the rest of the spore exine, sculptured by radial muri, 0·5–1 μ wide, slightly tapered and sinuous, usually 12 per interradial area; contact areas delimited by curvaturae perfectae which frequently coincide with the equator; distally exine smooth, homogeneous, 1–1·5 μ thick. Triradiate mark distinct, lips nearly equal, or equal to the spore radius.

Comparison and remarks. The muri of the Dittonian specimens appear to be relatively finer than those figured by Vigran 1964, however in the small size of the spores and the presence of curvaturae they are similar. *E. minutus* Allen 1965 is also very similar but *E. neglectus* Vigran has priority. Curvaturae are not recorded by Allen, however, the figured specimen (Allen, pl. 97, fig. 20) may have curvaturae which approximate to the equator in polar compression. *Leiotriletes*(?) *actinomorphus* Chibrickova 1962 is also similar but apparently lacks curvaturae.

Downtonian specimens have broader rather indistinct ribs; they resemble *Retusotriletes* cf. *minor* (see above) except for the faint proximal radial rib development.

Emphanisporites sp. A

Plate 39, fig. 1

Occurrence. Dittonian, Dairy Dingle, rare; Gedinnian.

EXPLANATION OF PLATE 39

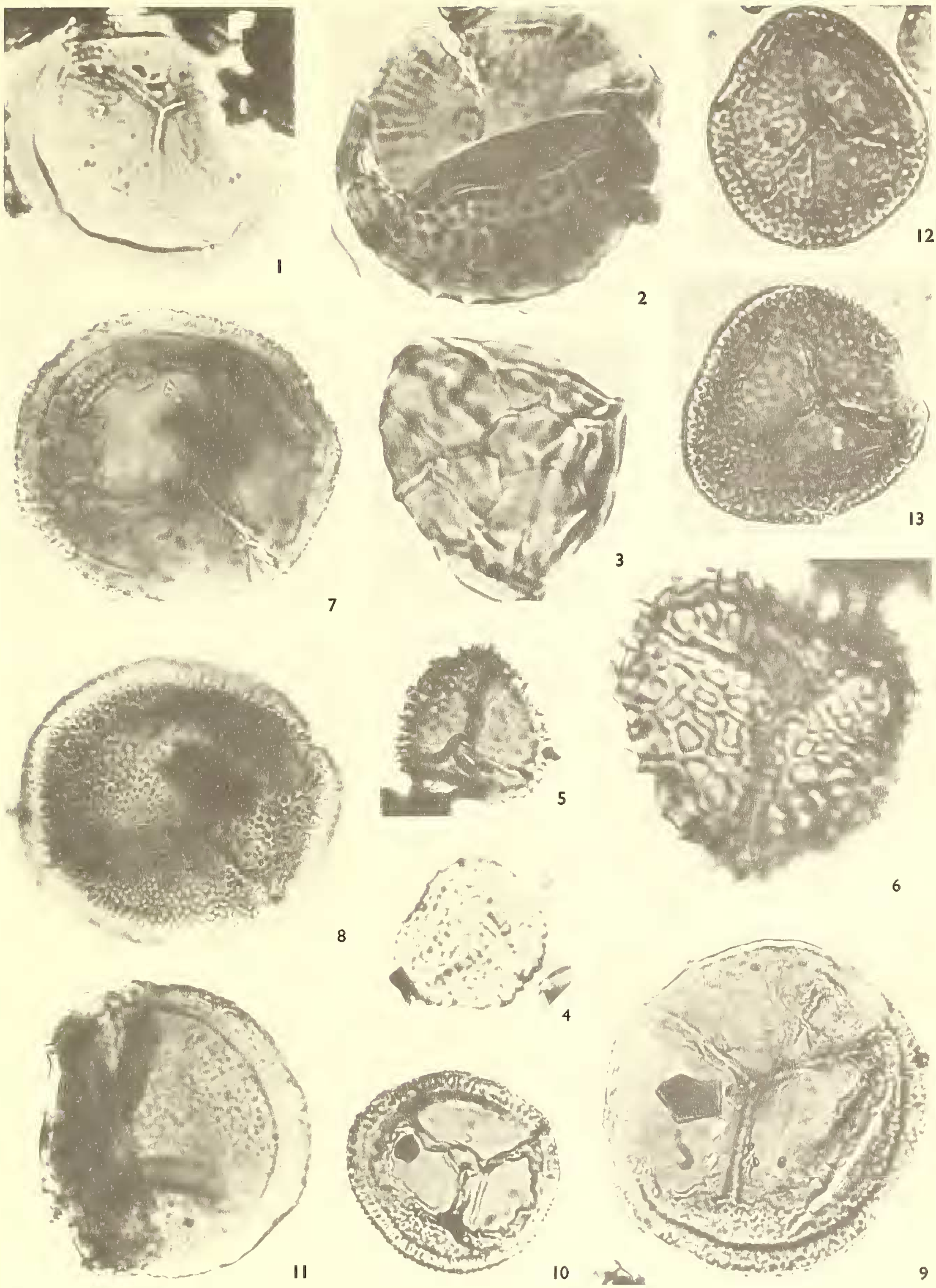
All figures ×1,000, and from Ditton Group, except where stated otherwise.

Figs. 1–2. *Emphanisporites* spp. 1, *E.* sp. A; tipped specimen showing thick exine over distal hemisphere, ×2,000; WB 128/370893. 2, *E.* sp. B; tipped specimen showing proximal ribs and distal cones; WB 128/418892.

Fig. 3. *Dictyotriletes* sp. A; specimen showing coarse reticulum and low muri; WB 126/374941. 4, ?*Dictyotriletes* sp. B; specimen showing fine reticulum and ? Y-mark, ×2,000; Downton Castle Sandstone Group, WB 48/367869.

Figs. 5–6. *Acinosporites salopiensis* sp. nov.; holotype. 5, Proximal focus showing Y-folds. 6, Distal surface focus showing reticulum, ×2,000.

Figs. 7–13. *Perotrilites microbaculatus* sp. nov. 7–11. *P. microbaculatus* var. *microbaculatus* sp. et var. nov. 7–8, Holotype. 7, Proximal focus showing separation of outer membrane, and smooth proximal surface. 8, Distal focus showing fine sculpture. 9, Tipped specimen showing small folds in 'perine' over contact areas; WB 128/417943. 10, Specimen with coarser sculpture; WB 140/442849. 11, Lateral compression showing thick exine (inner layer) over distal hemisphere; WB 135/453992. 12–13. *P. microbaculatus* var. *attenuatus* var. nov. 12, Holotype, proximal view. 13, Tipped specimen showing folding of 'perine' around margins of contact areas and thin exine (inner layer) over distal hemisphere; WB 167/427841.



RICHARDSON and LISTER, Devonian miospores

Description. Size range 40–50 μ (7 specimens measured). Amb circular to subcircular. Exine variable in thickness, 4–4·5 μ thick distally, 2–2·5 μ at equator; contact areas distinct, delimited by distinct curvaturae perfectae; which form small ridges 0·5 μ wide; contact areas with fine radiating 'muri' 1 μ wide, around 13 on each contact face, some of the 'muri' reach the spore apex. Triradiate mark distinct, sutures $\frac{2}{3}$ spore radius.

Comparison and remarks. This form differs from described species of *Emphanisporites* by the variable thickness of the exine. They are identical to *Retusotriletes dittonensis* sp. nov. except for the possession of fine proximal radial muri.

Emphanisporites sp. B

Plate 39, fig. 2

Occurrence. Ditton Group, Dittonian. Gedinnian, rare.

Description. Size range 36–54 μ (15 specimens measured). Amb subcircular, proximally slightly concave; most frequently seen in oblique compression, with strongly convex distal surface. Exine relatively thick 2·5–3 μ, proximally sculptured with radial muri 1–2 μ wide, rounded in profile, in plan taper gradually to proximal pole; bounded by distinct curvaturae perfectae. Distally sculptured with low, broad-based cones, verrucae to rugulae, rounded or pointed in profile, rounded to polygonal to elongate and irregular in plan, elements 0·5–1·5 μ high, 2–4 μ wide. Triradiate mark equals radius, sutures accompanied by low lips.

Comparison. Emphanisporites sp. B is distinguishable from *E. decoratus* Allen 1965 by broader and lower sculptural elements, of coni, verrucae, and rugulae; and from *E. micrornatus* sp. nov. by the greater size of the sculptural elements. *E. verrucatus* Lanninger 1968 has two coarse radial muri in each interradial area and thick lips.

Genus ACINOSPORITES Richardson 1965

Acinosporites salopiensis sp. nov.

Plate 39, figs. 5–6

Holotype. Size 27 × 29 μ; slide WB 127, ref. 384938; Ditton Group, Dairy Dingle; Gedinnian.

Occurrence. As above; rare.

Diagnosis. Spores small with well-marked contact areas and a distal reticulum; muri intersections bear small cones or spines.

Description. Size range 21–39 μ (30 specimens measured), mode 26 μ. Amb subtriangular, hemispherical in lateral view. Proximal surface smooth, exine 1–1·5 μ thick, homogeneous. Distal surface covered with a fine reticulum, discontinuous in some specimens but usually completely developed, muri of equal width and height 0·5–1 μ, lumina 1–2·5μ, at the intersections muri bear distinct cones or spines typically with stout bases and fine pointed apices, elements 0·5–1 μ wide, 1–6 μ long (length typically 1·5–2 μ). Triradiate mark distinct accompanied by lips 1 μ high, equal to spore radius, in obliquely compressed specimens lips merge with curvaturae perfectae which coincide with the equator.

Comparison. Dictyotriletes minor Naumova (1953) has a similar size range (20–30 μ) and appears spiny but lacks the prominent lips and has lumina 6 μ wide. The fact that the spores have spines superimposed on the reticulate muri excludes them from the genus *Dictyotriletes*. *A. macrospinosus* Richardson 1965 is much larger, has a distinct apical prominance, bears large spines, and has a more irregular reticulum.

Genus DICTYOTRILETES (Naumova) Potonié and Kremp 1954
Dictyotriletes sp. A

Plate 39, fig. 3

Occurrence. Ditton Group, Dairy Dingle; Gedinnian, rare.

Description. Size 21–4 μ on two specimens. Amb subtriangular. Exine less than 1μ thick, homogeneous, infragranular to granular. Proximal surface smooth to wrinkled. Distal surface covered with a broad reticulum, muri 0·5 μ high and of similar width, lumina 3–7 μ (5–7 and 3–6 respectively). Triradiate mark distinct equals spore radius, accompanied by low lips.

Comparison. Acinosporites salopiensis has spines and a reticulum with small lumina. *D. minor* Naumova (1953, pl. 2, fig. 7) has coarser muri and possibly has spines.

? *Dictyotriletes* sp. B

Plate 39, fig. 4

Occurrence. Ludlovian, Lower Downtonian, Linton Quarry, and Ditton Group, Dairy Dingle, Dittonian (Gedinnian). Rare.

Description. Size 13–19 μ (on six specimens). Dittonian specimen 25 μ. Amb subtriangular. Exine covered by a fine reticulum. Muri 0·5 μ, width more or less equal to height, lumina 0·5–3 μ. Most of the specimens show an apparent triradiate mark accompanied by smooth low lips 1 μ wide.

Remarks. These specimens are very small and it is difficult to determine if the 'suture and lips' are primary tetrad scars or are fortuitous cracks and associated folds, the latter are seen in four of the six specimens. Hence the spores are tentatively assigned to *Dictyotriletes*.

Subturma: PERINOTRILETES Erdtman 1947
Genus PEROTRILITES (Erdtman) Couper 1953
Perotrilites microbaculatus sp. nov.

Holotype. Size 52×54 μ; slide WB 133, ref. 4111031; Ditton Group, Dairy Dingle, Gedinnian.

Diagnosis. Outer layer, 'perine', thin, diaphanous, closely attached to the exine except over the proximal face, sculptured except over the contact area, by closely packed small rods, grana, or cones; inner layer, exine, relatively thick, distally thickened. Contact areas distinct.

Comparison. The close attachment of the 'perine' except over the contact areas, distinguishes this species from most other spores assigned to this genus. *Diaphanospora* *apiculata* Guennel 1963 has a tightly fitting perine but it lacks the well-defined contact areas and has more sparsely distributed sculpture.

Perotrilites microbaculatus var. *microbaculatus* var. nov.

Plate 39, figs. 7–11

Holotype and occurrence. Same as species *microbaculatus*.

Diagnosis. 'Perine' forms prominent folds around the margins of the contact areas, frequently wrinkled or folded over the contact areas, distally sculptured by microbaculae; exine relatively thick, thickness at the equator 2–3·5 μ, distally 3–6 μ.

Description. Size range 28–64 μ (100 specimens measured), mode 51 μ. Amb subcircular to subtriangular, hemispherical in lateral view with flattened proximal surface. 'Perine' and exine closely attached except over the contact areas; 'perine' thin diaphanous sculptured except over the contact areas. Sculpture of microbaculae, minute and frequently difficult to resolve, elements dominantly parallel-sided and flat-topped but some elements expand at their apices; microbaculae less than 0·5–1 μ high, 0·5 μ or less, wide. Exine thick, thickest over the distal pole, homogeneous, smooth. Contact areas distinct. Trilete sutures distinct on the exine, $\frac{3}{4}$, equal or nearly equal to the spore radius; prominent trilete folds occur in the 'perine'.

Comparison and remarks. The thick exine, size mode and sculpture distinguish this variety from *P. microbaculatus* var. *attenuatus* var. nov.

The variable thickness of the exine can clearly be seen (Plate 39, figs. 9 and 11). *Retusotriletes dittonensis* sp. nov. has a similarly thickened exine and size range and it it possible that spores of the latter species are the inner bodies (exines) of *P. microbaculatus* var. nov. which have lost their 'perine'.

Perotrilites microbaculatus var. *attenuatus* var. nov.

Plate 39, fig. 12–13

Holotype. Size 34 × 38 μ; slide WB 167, ref. 301864; Ditton Group, Dairy Dingle, Gedinnian.

Occurrence. As above.

Diagnosis. 'Perine', closely adhering to the exine, forms small folds around the contact areas; distally sculptured by microbaculae, coni or grana; exine 0·5–2 μ thick at the equator, distally 2–3 μ.

Description. Size range 27–48 μ (100 specimens measured), mode 33 μ. 'Perine' and exine closely attached except over contact areas. Sculpture distinct reduced on the proximal surface and absent over the contact areas; elements vary from being minute and difficult to resolve to relatively coarse; they consist of microbaculae with flat apices, or grana, and coni; elements typically about 0·5–1 μ high, 0·5 or less to 1 μ wide. In all other respects closely comparable to *P. microbaculatus* var. *microbaculatus* var. nov.

Comparison. The thinner exine, size mode, generally slightly coarser sculpture and more closely attached 'perine' distinguishes this variety.

? *Perotrilites* sp. A

Plate 40, fig. 1

Occurrence. Lower Downtonian, Linton Quarry, Downton Gorge, Long Mountain. Rare.

Description. Size range 37–50 μ (6 specimens). Amb subtriangular. Spores two-layered, outer layer ('perine') thin, diaphanous, exine 2·5–4 μ thick, thinner in the interradial areas. 'Perine' smooth, loosely attached and folded. Exine smooth to occasionally slightly undulose. Triradiate folds on the 'perine' reach the equator.

Remarks. In the thick exine and the relatively thin outer layer ('perine') these spores resemble other species placed in the genus *Perotrilites*. There are a number of spore species in Downtonian and Dittonian strata in which occasional specimens show an adhering diaphanous layer which is sometimes fragmentary. So in general appearance and preservation they resemble perine of modern spores. Similar spores but with a more closely attached 'perine' occur in the Dittonian.

Subturma ZONOTRILETES Waltz 1935
Infraturma CRASSITI Bharadwaj and Venkatachala 1961
Genus AMBITISPORITES Hoffmeister 1959

Type species. A. avitus Hoffmeister 1959.

Remarks. The spores described below are tentatively left in the genus *Ambitisporites* Hoffmeister 1959 and not placed in *Stenozonotriletes* (Naum.) Potonié 1958 or *Asterocalamotriletes* (Luber) Potonié 1958 because of the uncertain status of these two genera. All are defined on the basis of being smooth-walled and having a narrow zone of equatorial thickening (crassitude).

In *Stenozonotriletes* however this is apparently not the case since the figured specimen of the type species (*S. conformis* Naumova 1953, pl. 3, fig. 15) does not appear to have

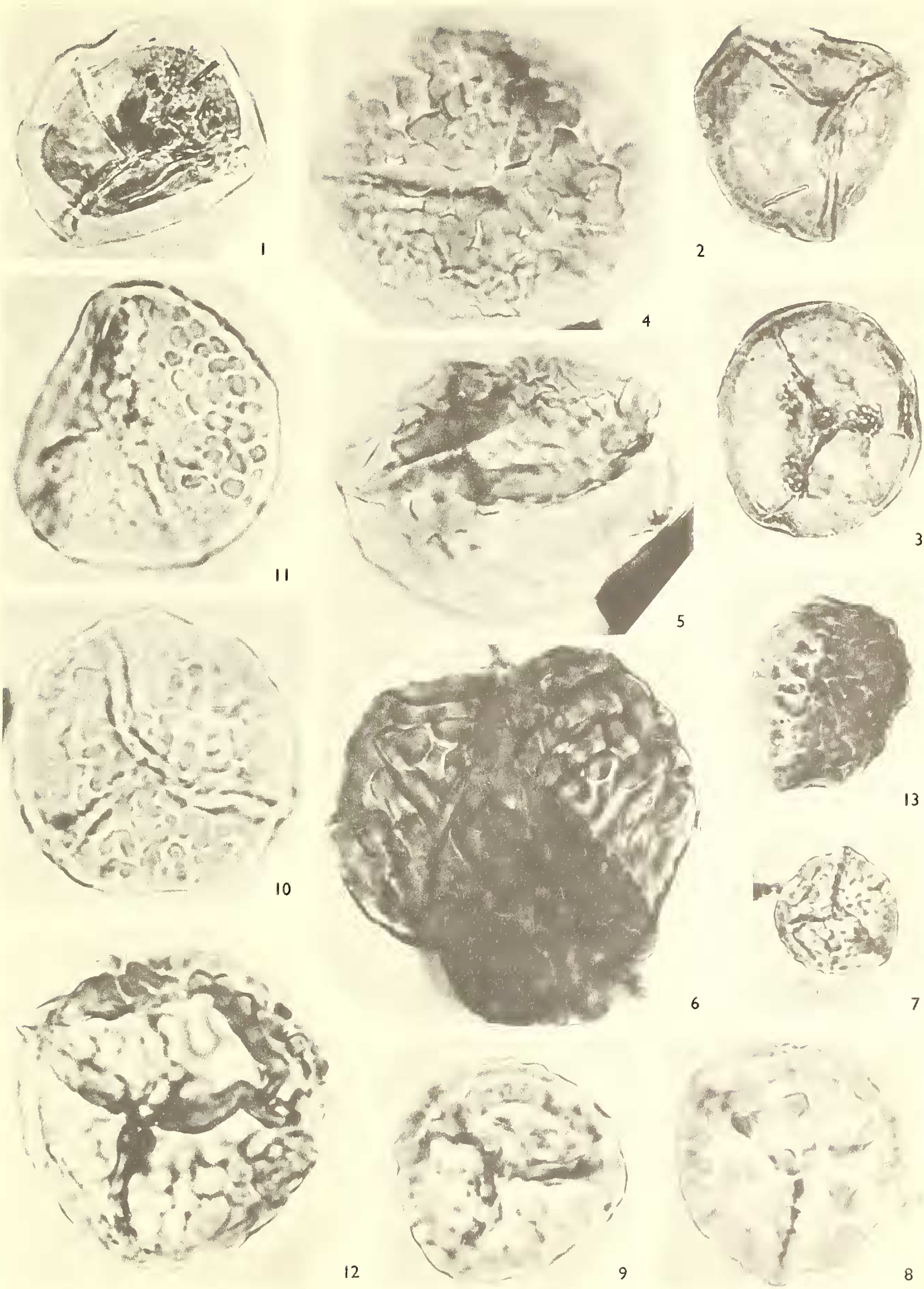
EXPLANATION OF PLATE 40

All figures ×1,000 except where stated otherwise.

Fig. 1. ?*Perotrilites* sp. A; Downton Castle Sandstone Group, WB 29/458943.

Figs. 2–3. *Ambitisporites* spp. 2, *A.* cf. *avitus* (Hoffmeister) 1959; Wenlock Shale (Tickwood Beds), MPK 7. 3, *A.* cf. *dilutus* (Hoffmeister) comb. nov.; Lower Elton Beds, MPK 5.

Figs. 4–13. *Synorisporites* gen. nov. 4–5. *S. downtonensis* sp. nov. 4, Holotype, distal view showing convolute muri. 5, Lateral compression showing thickened curvaturae perfectae and finer proximal muri; Downton Castle Sandstone Group, WB 30/289908. 6, Cf. *S. downtonensis* sp. nov.; tetrad, Lower Bringewood Beds, MPK 10. 7–9. *S. tripapillatus* sp. nov. 7–8, Holotype. 7, Proximal focus showing papillae. 8, Distal focus showing convolute muri, ×2,000. 9, Tipped specimen showing thickened curvaturae perfectae, ×2,000; Downton Castle Sandstone Group, WB 33/453875. 10–12. *S. verrucatus* sp. nov., ×2,000. 10, Holotype, distal focus showing sculpture of verrucae and muri. 11, Distal focus showing discrete verrucae; Downton Castle Sandstone Group, WB29/359941. 12, Tipped specimen showing thickened curvaturae perfectae; Downton Castle Sandstone Group, WB 62/2641051. 13, Cf. *S. verrucatus* sp. nov., lateral compression (proximal surface not preserved); Lower Elton Beds, MPK 11.



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any equatorial thickening. Similarly the nature of the genus *Asterocalamotriletes* is also uncertain both from the original drawings (Luber 1955, pl. 1, 8–9) and description.

The exine of the spores described below is laevigate. The type species, however, is described as 'laevigate to faintly granular', but no sculpture can be seen in Hoffmeister's illustrations and it is possible that the observed faint granulation is either infrastructure or due to preservation. In this paper smooth-walled spores with an equatorial crassitude are tentatively assigned to *Ambitisporites* pending clarification of *Stenozonotriletes*, forms with distinct granulate–apiculate sculpture in the genus *Streelispora* gen. nov., and verrucate–murinate forms in the genus *Synorisporites* gen. nov.

In all these spores the crassitude delimits the margin of the contact areas and diverges from the trilete mark, i.e. it is curvaturate. In polar compression, however, the trilete reaches or rarely nearly reaches the equator and it is only in the latter that the thickenings do not coincide with the equator at the radial apices. Consequently although the thickenings are curvaturate they form essentially an equatorial structure and therefore these genera are placed in Infraturma Crassiti.

Ambitisporites cf. *dilutus* (Hoffmeister) comb. nov.

Plate 40, fig. 3

cf. 1959 *Punctatisporites* ? *dilutus* Hoffmeister, p. 334, pl. 1, figs. 9–13.

Occurrence. Wenlock shale, Wenlock Limestone, Elton beds, and ? present Upper Whitcliffe beds.

Description. Size range 28–40 μ (14 specimens measured). Essentially comparable with Hoffmeister's spores except that lips are developed in some of the specimens. In the range charts spores lacking lips are referred to as *Ambitisporites dilutus* sensu stricto.

Comparison and remarks. The equatorial crassitude is also present in *Ambitisporites avitus* (Hoffmeister 1959, pl. 1, fig. 4), and although in the latter the thickening is much more pronounced it is possible that these two species intergrade. However, only rare specimens resembling *Ambitisporites avitus* (Pl. 40, fig. 2) have been found in the present study.

There are also broad similarities between spores of the *avitus-dilutus* complex and the species *Archaeozonotriletes chulus* (Cramer). However, the latter typically has a thicker distal-equatorial wall and a thin proximal wall which is frequently folded into taper-pointed folds or collapsed.

In the succession studied forms resembling the *avitus-dilutus* complex typify the lowest part of the sequence (Wenlock Shale) whereas higher in the Silurian, and in the Lower Devonian, spores of *A. chulus* are typical and only a few spores doubtfully resembling *avitus-dilutus* spp. occur. The specimen figured by Downie (1963, pl. 92, fig. 13) has lips and is therefore closely similar.

Cramer (1966) figured three spores which he referred to the species *Ambitisporites avitus* Hoffmeister 1959. One of Cramer's spores (pl. 2, fig. 15) has a narrow darkened border resembling that of *A. dilutus* (Hoffmeister). Another specimen (pl. 2, fig. 13) has strong triradiate folds and is similar to the specimens herein referred to as *A.* cf. *avitus* (Pl. 40, fig. 2).

Genus STREELISPORA gen. nov.

Type species. Streelispora newportensis (Chaloner and Streel) comb. nov.

Diagnosis. Radial, trilete, spores with a more or less equatorial crassitude which delimits distinctive contact areas. Spores distally sculptured with grana, coni, spinae or biform elements. Proximally smooth, or with interradial papillae, or variously sculptured.

Comparison and remarks. This genus is similar to Streel's concept of *Aneurospora* Streel 1964. However Streel (1967, p. 47) now considers that the type species *A. goensis* Streel 1964 belongs to the genus *Geminospora*. Transfer of the type species necessitates the creation of a new genus for the spores described below.

Cadiospora Kosanke 1950 has thickened lips and lacks prominent sculpture. In *Lycospora* the thickenings are more distinct, clearly wedge-shaped, and project at the equator. Further the type species shows a clear 'flange' development (Wilson and Coe 1940, pl. 1, fig. 6) in contrast to the narrow crassitude of *Streelispora*. Smith and Butterworth (1967) stress the wedge-shaped and projecting nature of the cingulum in distinguishing *Lycospora* from *Stenozonotriletes*. They state (p. 216) that *Stenozonotriletes* differs from *Lycospora* and *Denosporites* in that in polar section the cingulum is of more or less uniform thickness and does not show any flange development. This seems a reasonable basis for subdivision but at present a wide range of forms are placed in the genus *Lycospora* and there appears to be some overlap between it and the genus *Stenozonotriletes*. Smith and Butterworth tentatively place forms with sculpture in the genus *Stenozonotriletes* (? *Stenozonotriletes bracteolus*, p. 217); however this genus should be restricted to laevigate and punctate spores and forms like ? *S. bracteolus* should probably be assigned to *Streelispora* gen. nov. The situation is further complicated by the uncertain status of the genus *Stenozonotriletes* (see p. 228 above).

Streelispora newportensis (Chaloner and Streel) comb. nov.

Plate 41, figs. 3–6

1968 *Granulatisporites newportensis* Chaloner and Streel, p. 92, pl. 19, figs. 7–8.

Holotype. Chaloner and Streel 1968, slide no. PF 3239. Lower Ditton Group, Newport, south Wales. Lower Gedinnian.

Occurrence. Ditton Group as above and Dairy Dingle; ? Senni Beds, Llanover.

Emended diagnosis. Equatorial crassitude 1–2 μ wide. Proximal surface with three interradial papillae surrounded by tangential and radial folds, exine over proximal surface thin, distally sculptured by coni or biform coni.

Description. Size range 17–48 μ; Dairy Dingle specimens 17–34 μ (80 specimens measured), mode 28 μ. Amb triangular with convex sides and rounded apices, usually compressed in polar view, spores originally hemispherical with flattened pyramidal proximal surface. Exine homogeneous 0·5–1·5 μ thick distally. Contact areas highly distinctive, bear three relatively large papillae, one in each interradial area, papillae circular in plan, rounded in profile, 3–4 μ wide, folds surround the papillae, most prominent folds roughly parallel equator, but frequently other folds occur at right angles to these. Distinct to barely distinguishable equatorial crassitude 1–2 μ wide, $\frac{1}{15}$–$\frac{1}{6}$ of the spore radius. Sculpture confined to the equatorial margin and distal surface, elements consist of coni, with rounded to pointed apices, occasionally biform with sharply tapered basal portion tipped by slender cones; width 0·5–2μ, height 0·5–1 μ, elements typically spaced 0·5–2 μ apart, rounded in plan. Triradiate mark distinct, sutures equal spore radius, accompanied by lips 0·5–1 μ wide.

Comparison and remarks. S. granulata sp. nov. has a thicker exine and sculpture of grana and small cones rather than cones and biform elements. The folds which surround and radiate from the large proximal papillae may be due to shrinkage of a proximal membrane which is relatively thin except in the region of the interradial papillae, however they form a constant feature. The proximal polar area typically appears thinner than the rest of the exine (Pl. 41, fig. 3).

Specimens described by Chaloner and Streel have been re-examined and are essentially the same as the specimens from Dairy Dingle. However specimens from the latter locality tend to have larger, more widely spaced sculptural elements, a thicker distal wall and more distinct crassitude (Pl. 41, figs. 5 and 6).

Streelispora granulata sp. nov.

Plate 41, figs. 7–9

Holotype. Size 28×29 μ, slide WB 135, ref. 409932, Ditton Group, Dairy Dingle, Gedinnian.

Occurrence. ? Present Ludlovian, Ludlow, and Lower Downtonian, Ludford, Downton Gorge and Gorsley Common; Ditton Group as above.

Diagnosis. Exine relatively thick, equatorial crassitude thicker in the interradial areas, 2–4 μ, than radially 1·5–2·5 μ; distally sculptured by closely packed grana.

Description. Size 18–34 μ (40 specimens measured), mode 28 μ. Amb subtriangular with convex sides and rounded apices. Original lenticular shape indicated since almost invariably preserved in polar compression. Proximal face smooth or occasionally bears three interradial papillae, around 4 μ in diameter; exine at the equator and distally covered with small coni or grana; elements circular to subcircular in plan, rounded to pointed in profile; width 0·5–1 μ, height of elements equal to or somewhat less than width, typically around 0·5 μ, elements spaced 0·5–1 μ apart. Triradiate mark distinct, rays equal or nearly equal to spore radius; occasionally accompanied by low lips.

Comparison. The thick exine and its variable thickness at the equator distinguishes this species. *Granulatisporites muninensis* Allen 1965 has a thinner exine. *Retusotriletes multituberculatus* Lanninger 1968 is much larger (75 μ) and has sparser sculptural elements. '*Levigatisporites*' *munstereifeliensis* Franke 1965 appears similar but the figured specimens (pl. 3, figs. 43 and 44) have an apical thickening and are too poorly preserved to make precise comparisons.

Remarks. The Ludlovian and Downtonian specimens are poorly preserved, they have a thick exine but it has not proved possible to determine whether this is thicker in the interradial areas, consequently these spores are referred to as cf. *Streelispora granulata.*

Genus SYNORISPORITES gen. nov.

Type species. Synorisporites downtonensis sp. nov.

Diagnosis. Radial, trilete spores with prominent curvaturae perfectae forming a more or less equatorial crassitude. Contact areas distinct, smooth, or with interradial papillae, or variously sculptured; distally sculptured with verrucae and/or, muri.

Comparison and remarks. Streelispora gen. nov. is structurally similar but has a distal ornament of grana, coni, spinae, or biform elements.

Synorisporites downtonensis sp. nov.

Plate 40, figs. 4–5

Holotype. Size 52 × 58 μ; slide WB 32, ref. 3991063; Lower Downtonian, Linton quarry.

Occurrence. Lower Downtonian, in all samples studied from Gorsley Common, Ludford, Downton Gorge and Long Mountain.

Diagnosis. Distal sculpture of relatively large, convolute, and anastomosing muri, curved in plan and rounded in profile; proximal sculpture consists of smaller muri more angular in plan but rounded in profile.

Description. Size range 44–78 μ (120 specimens measured), mode 58 μ. Amb subtriangular with convex sides and rounded apices. Spores usually preserved in polar compression suggesting an original of more or less lenticular shape. Exine homogeneous, at equator and distally 2–3 μ thick, excluding muri. Contact areas distinct, sometimes depressed; crassitude 4–5 μ wide, in lateral compression only extends slightly at the equator; crassitude equatorially and distally smooth, proximally ridged, ridges tend to be radially arranged and merge into proximal muri. Contact areas covered with irregular convolute muri somewhat angular in plan, rounded to conical in profile; muri diminish in size towards apex which is relatively smooth in some specimens; proximal muri 0·5–3 μ wide (typically 1–2 μ). Distal surface covered by convolute and anastomosing

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EXPLANATION OF PLATE 41

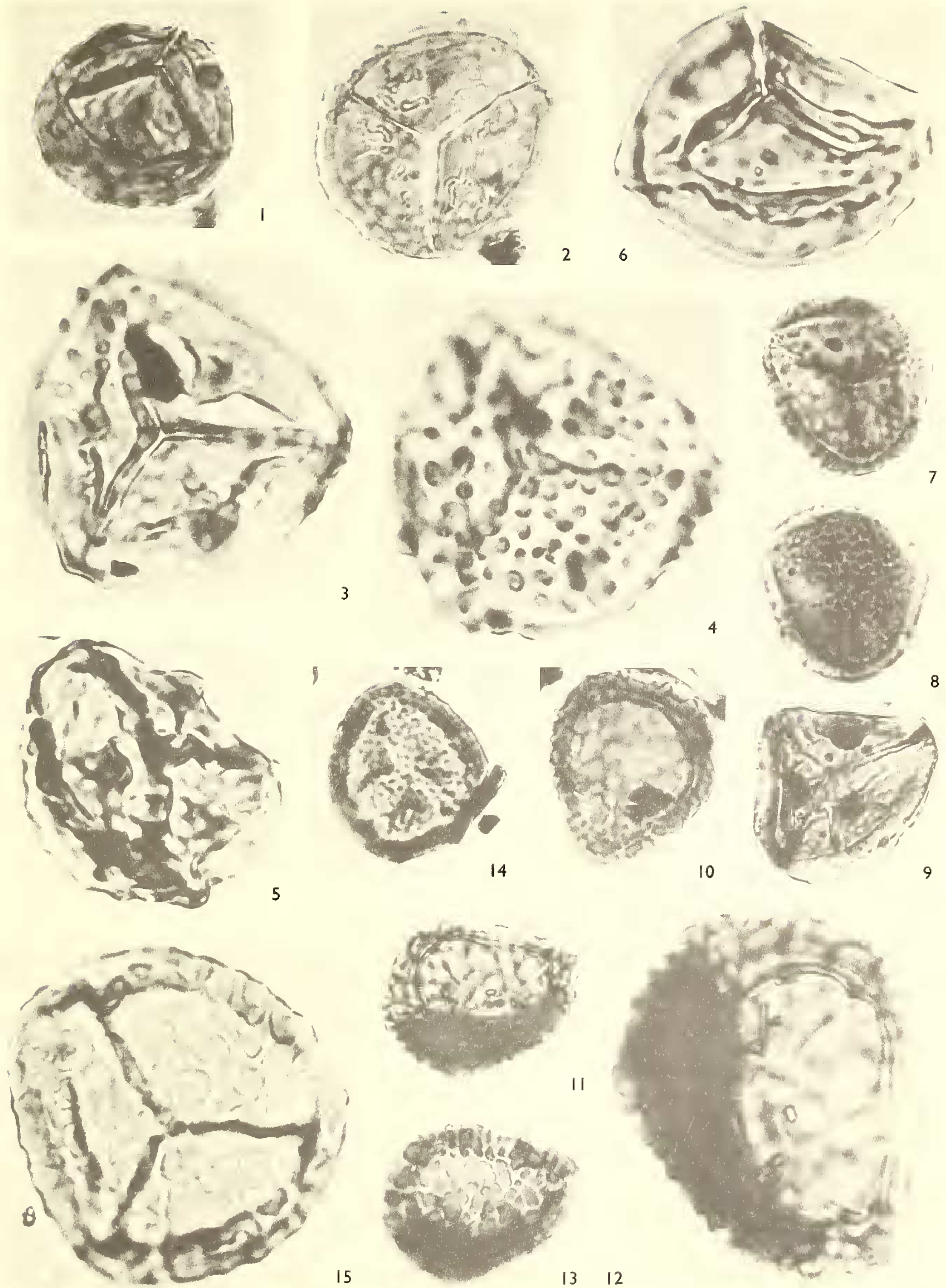
All figures × 1,000 except where stated otherwise and all from the Ditton Group.

Figs. 1–2. *Synorisporites* sp. A. 1, Tipped specimen showing distal sculpture, proximal papillae and curvaturae perfectae; WB 125/4281052. 2, Proximal surface; infra-structure WB125/308860.

Figs. 3–9. *Streelispora* gen. nov. 3–6. *S. newportensis* (Chaloner and Streel) comb. nov., × 2,000. 3–4, Polar view; WB 126/4111009. 3, Proximal focus, showing tangential folds around proximal papillae. 4, Distal focus showing sculpture of cones. 5, Tipped specimen showing thickened curvaturae perfectae and proximal papillae; WB 135/368909. 6, Lateral compression showing curvaturae perfectae with projecting cones; WB 135/446962. 7–9. *S. granulata* sp. nov. 7–8, Holotype. 7, Proximal focus showing variable thickness of exine. 8, Distal focus showing sculpture. 9, Tipped specimen with proximal papillae; WB 135/331977.

Figs. 10–14. *Cymbosporites* spp. 10–13. *C. dittonensis* sp. nov. 10, Holotype, polar compression. 11–13, Lateral compression at different focus levels. 11, Showing thin proximal area, concentric fold around contact areas, and thick distal patina. 12, Same, × 2,000. 13, Showing sculptural elements. 14, *C.* cf. *catillus* Allen 1965, polar compression; WB 135/4301018.

Fig. 15. ?*Chelinospora* sp. A, showing contact areas, distal and equatorial muri, × 2,000; WB 135/432918.



RICHARDSON and LISTER, Devonian miospores

muri, 2–4·5 μ wide (typically 2·5–3·5 μ), and 1–2 μ high, usually closely packed but occasionally well spaced. Triradiate mark distinct, sutures $\frac{4}{5}$ to equal spore radius, accompanied by elevated lips, 1·5–2 μ wide, 2·5–4·5 μ high, lips have crenulate outer margins.

Comparison and remarks. S. tripapillatus sp. nov. is smaller and has prominent interradial papillae. *S. verrucatus* is distally verrucate–murinate. Similar spores occur sparsely in the Lower Ludlow (Pl. 40, fig. 6); unfortunately the best specimens are in tetrads and the details of the proximal face have not been seen. Consequently these spores are tentatively referred to as cf. *S. downtonensis* in the text.

Synorisporites tripapillatus sp. nov.

Plate 40, figs. 7–9

Holotype. Size 20 × 20·5 μ; slide WB 28, ref. 462977; Lower Downtonian, Linton Quarry.

Occurrence. Lower Downtonian, occurs in all samples, relatively abundant.

Diagnosis. Spores small with distal sculpture of convolute muri and proximal surface bearing three papillae, one in each interradial area.

Description. Size range 10–28 μ (150 specimens measured), mode 18 μ. Amb triangular, with convex sides and rounded apices; probably originally more or less hemispherical in shape, only rarely seen in oblique compression. Exine 1–1·5 μ thick. Sculpture distinct convolute and anastomosing muri which are 1–2 μ wide, 0·5–1 μ high. Contact areas distinct, appear thinner than the rest of the spore exine, equal to, or slightly less than, the proximal surface; bounded by curvaturae perfectae forming an indistinct, more or less equatorial, crassitude 2–3 μ wide; proximal papillae circular in plan, rounded in profile, 1·5–3 μ in diameter, typically 2·5 μ, contact areas otherwise smooth. Triradiate mark accompanied by folds which reach the equatorial margin.

Comparison and remarks. The small size and interradial papillae distinguish this species from *S. downtonensis* sp. nov. Papillae are a constant feature but are sometimes indistinct.

Synorisporites verrucatus sp. nov.

Plate 40, figs. 10–12

Holotype. Size 24 × 24 μ; slide WB 62, ref. 3821009; Lower Downtonian, Linton Quarry.

Occurrence. Lower Downtonian, occurs in all samples studied; ? present in '*Psammosteus*' Limestone.

Diagnosis. Proximal face smooth, distally sculptured dominantly by small verrucae occasionally fused into small groups.

Description. Size range 16–33 μ (100 specimens measured), mode 23 μ. Amb subtriangular; spores usually preserved in polar compression indicating originally lenticular with flattened pyramidal proximal surface. Exine homogeneous 1·5–2 μ thick distally. Proximal face smooth. Contact areas distinct delimited by distinct curvaturae perfectae only slightly thickened, forming an equatorial crassitude 2–3 μ wide in polar compression; crassitude proximally and distally smooth. Distal surface sculptured dominantly by verrucae 1–4·5 μ wide (typically 2 μ but size variable in a single spore), 0·5–1·5 μ high; verrucae rounded, subangular, polygonal, irregular, slightly indented and elongate, occasionally fused into small groups to give a murinate appearance, muri and verrucae can occur on the same specimen but verrucae are dominant; in profile elements rounded to truncate with more or less parallel sides; elements spaced usually 0·5 μ apart. Triradiate mark distinct equal to spore radius, accompanied by lips up to 3 μ high.

Comparison. Synorisporites tripapillatus is smaller and has a distal sculpture of convolute and anastomosing muri, and three proximal interradial papillae. The sculpture of *S. verrucatus* is dominantly verrucate although on some specimens the verrucae are joined up to form short muri, discrete verrucae, however, occur along with the muri; further the proximal face of *S. verrucatus* sp. nov. is smooth and has no interradial papillae.

Spores with similar verrucate–murinate sculpture occur sporadically through the Ludlovian and a single specimen in the Wenlock (different from the Ludlow specimens). Unfortunately in the Silurian spores the proximal face is not well preserved and consequently these spores are tentatively referred to as cf. *S. verrucatus* sp. nov. (Pl. 40, fig. 13). The holotype of *Chelinospora vermiculata* Chaloner and Streel (1968, pl. 20, figs. 7–8) is similar in construction and may be a corroded specimen of *A. chulus* (Cramer).

Synorisporites sp. A

Plate 41, figs. 1–2

Occurrence. Ditton Group, Dairy Dingle, Gedinnian.

Description. Size range 30–45 μ (15 specimens measured). Amb subcircular, in lateral view hemispherical. Exine 2–3·5 μ thick. Contact areas distinct delimited by distinct curvaturae perfectae only slightly thickened, which coincide with the equator for all their length, except in the radial apices; curvaturae clearly seen in obliquely compressed specimens. Proximal surface bears three interradial papillae, circular darkened areas 3·5 μ wide, otherwise externally smooth but with distinct infrastructure of polygonal to radial elements. Equatorially and distally covered with verrucae which are rounded, subangular to elongate, 1–5 μ wide, 0·4–1 μ high, and typically 0·5–1 μ apart. Some specimens appear two-layered. Triradiate mark distinct nearly equal, or equal, to spore radius, accompanied by lips 1 μ wide, lips confluent with curvaturae.

Comparison and remarks. Differs from *S. verrucatus* sp. nov. in its larger size, and presence of three proximal papillae. Similar specimens in the Downtonian lack the papillae, tend to be subtriangular, and have a smooth equatorial margin.

Infraturma PATINATI Butterworth and Williams 1958
Genus ARCHAEOZONOTRILETES (Naum.) Allen 1965

Type species. A. variabilis (Naum.) Allen 1965.

Archaeozonotriletes chulus (Cramer) comb. nov.

1966 *Retusotriletes chulus* Cramer, p. 74, pl. 2, fig. 14.

Holotype. Cramer 1966 (reference specimen) slide 224 (42), 118·1×35·7, pl. 2, fig. 14. Upper San Pedro Formation, León, Spain; Ludlovian-Lower Gedinnian.

Emended diagnosis. Trilete patinate spores, exine thin sometimes diaphanous in the contact areas, equatorially and distally thickened, narrow equatorial crassitude delimits contact area so that the exine thickness at the equator often exceeds that at the distal pole. Exine laevigate but may show a distinctive infrastructure of radial or convolute muri. Proximally thin contact areas frequently collapsed and the spores usually have a narrow concentric fold, simulating curvaturae, just inside the equatorial border.

Comparison. Retusotriletes chulus recently described by Cramer (1966) is clearly similar to spores from the Welsh Borderland although the latter show greater variety than those described by Cramer. However, Cramer's description is inadequate, no reference is made to spores of similar organisation, and no holotype is designated as such. In the circumstances rather than erect a new species for closely similar spores it seems preferable to extend Cramer's description and to establish Cramer's reference specimen as the holotype. *Ambitisporites avitus* and *Punctatisporites? dilutus* Hoffmeister 1959 appear to have a similar equatorial thickening, however, they can be distinguished from *A. chulus* (Cramer) since they lack the thin proximal face and thick distal wall (compare Pl. 43, fig. 4 with pl. 1, fig. 4 in Hoffmeister 1959). *Retusotriletes semizonalis* McGregor 1964 does not have the pronounced differential thickening between the proximal and distal surfaces of the spores described above and has minute sculpture.

Remarks. In polar compression the spores resemble spores of the genus *Ambitisporites* except that they have very thin contact areas. However, some tetrads and obliquely compressed specimens show clearly (Pl. 43, figs. 2–4) that the exine is much thicker at the equator and over the distal surface. Consequently these spores approximate more closely to the patinate genus *Archaeozonotriletes* (Naum.) Allen than to either *Ambitisporites* or *Stenozonotriletes*. The patina in these Silurian and Lower Devonian spores is uniformly thickened, or slightly thickened laterally. Allen distinguishes the two patinate genera *Archaeozonotriletes* (Naum.) and *Tholisporites* (Butterworth and Williams) on the basis of location of maximum thickness of the patina. *Archaeozonotriletes* (Naum.) is defined as having a uniformly, or distally, thickened patina whereas in *Tholisporites* the greatest thickness is equatorial. In practice without the aid of thin sections it may be very difficult to separate these two genera.

Archaeozonotriletes chulus var. *chulus* var. nov.

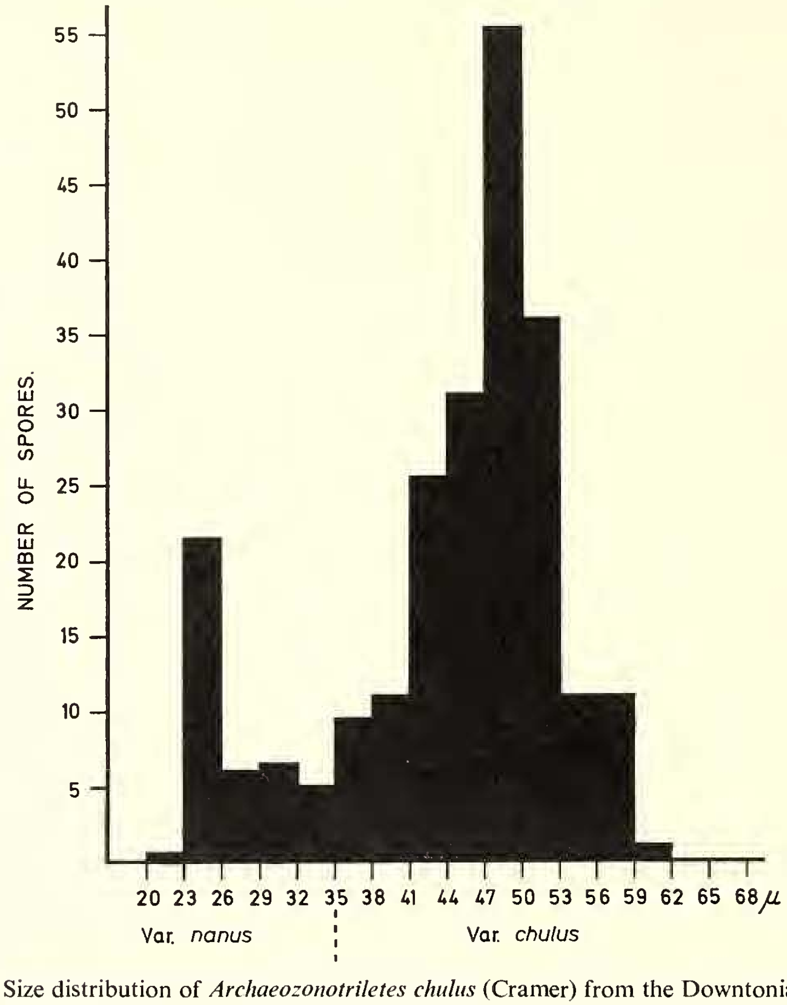
Plate 43, figs. 1–6; text-fig. 4

Holotype. As for species.

Occurrence. Deposits of Upper Ludlovian to Lower Gedinnian age, León Spain; Ludlovian, Lower Downtonian, in all samples from Gorsley Common, Ludford, Downton Gorge, and Long Mountain, Ditton Group, Dairy Dingle, and Senni beds, Breconshire, Ludlovian to ?Emsian.

Diagnosis. Size mode 48 μ, exine laevigate and lacks prominent infrastructure.

Description. Size range 36–60 μ (130 specimens measured). Downtonian and Dittonian specimens have identical modes and almost identical size ranges the latter are 36–58 μ and 38–60 μ respectively. Amb triangular with convex sides and rounded apices; hemispherical in lateral view. Exine over contact areas thin, approximately 1 μ in thickness, typically has a concentric fold just inside the spore margin, and occasionally there are taper pointed folds across the proximal face. Exine thickness at the equator more or less equal to exine over the distal pole but may be slightly greater or less. Downtonian specimens exine 3–6 μ at the equator, slightly thicker in the interradial regions 4–6 μ, distally 4–5 μ; Dittonian specimens exine 2·5–5 μ equatorially (typically 3·5–4·5 μ) somewhat less at the radial apices where there is frequently an invagination on the inner



TEXT-FIG. 4. Size distribution of *Archaeozonotriletes chulus* (Cramer) from the Downtonian–Dittonian of the Welsh Borderland.

margins of the exine; distally somewhat thinner, 2–2·5 μ. Exine smooth homogeneous although occasionally shows a tendency to break down. Triradiate mark $\frac{4}{5}$ to equal spore radius, lips form distinctly elevated folds 2–3 μ high; occasionally in Downtonian specimens the proximal pole exhibits a small triangular darkened area.

Remarks. The thickening of the exine at the equator which is seen in some Downtonian and Dittonian specimens is curvatural, however, in polar compression curvatural